Quantification of Insect Pollination, Natural Pest Control and their Synergies in Agricultural Ecosystems

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde (Dr. sc. nat.)

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultät

der

Universität Zürich

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Zürich, 2016

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SUMMARY

Nature provides a multitude of benefits to humans such as control of crop pests by their natural enemies or crop pollination by animals. These functions are known as ecosystem services and are of crucial importance for agricultural production. This thesis explores the potential of insect delivered ecosystem services, their interactions and consequences for crop yield through field surveys over 2 consecutive years in Swiss agricultural landscapes, combined with a controlled field realistic experiment. It aims; firstly, to determine the resource use of different bee target groups and to investigate whether ecological enhancement of herbaceous semi-natural habitats can foster several components of biodiversity; secondly, to quantify the strength and effects of ecological enhancement measures, at local and landscape scale, on ecosystem services delivery in agricultural fields and their potential consequences for crop yield; and thirdly, to test whether insect pollination and pest control are independent or synergistically interact, affecting crop yield, and additionaly estimate their monetary value.

Chapter 1 explores the relationship between the availability of food resources for different bee target groups in agro-ecosystems and the total and preferential use of these resources. In a field survey of bees in agricultural herbaceous semi-natural habitats, proportionally and disproportionally visited key plant species were identified for wild crop pollinators, rare bees, and honey bees. Although rare bees visited a subset of the plant species visited by other bee target groups, they showed a preference for a distinct set of plant species. Despite preferences for different plant species between bee groups, the abundance of all bee target groups was positively influenced by plant species richness at the same rate. Finally, the flower abundance of key plant species and the functional complementarity of the plant community were the determining factors for bee visits, rather than the total flower abundance. These results lead to the conclusion that plant species richness of semi-natural herbaceous

vegetation can foster different components of biodiversity, resulting in potential positive effects for different functions like ecosystem services and biodiversity conservation.

In **chapter 2,** insect pollination and natural pest control were measured as a function of the independent and interactive effects of locally established ecological focus areas and landscape-scale greening measures. Insect pollination and pest predation increased by 10% and 13%, respectively, when landscape-scale greening measures were increased. For pollination, the increase was stronger in fields next to an ecological focus area than in fields adjacent to another crop field. Agricultural management practices at field level were the main drivers of crop yield. Pest predation alone, but not pollination, enhanced yield by 9% at average management intensity, leading to the conclusion that the local establishment of ecological focus areas, combined with landscape-scale greening measures promote ecosystem services. The resulting benefits may be maximized when local and landscape measures are combined. These findings should encourage farmers to implement and maintain such beneficial habitats.

The study in **chapter 3** focused on potential interactions of ecosystem services. Until recently, ecosystem services were mostly studied in isolation, without taking into account potential interactions. However, in a field realistic controlled experiment, insect pollination, and simulated pest control revealed strong synergistic effects on crop yield. Their combined effect increased yield by 23%, with single service contributions of 7% and 6% respectively, whereas synergistic effects contributed 10%. The potential economic benefit was further increased by 12%, via an additional increase in yield quality, from the synergistic effects. This strong interaction between two ecosystem services, vital for global crop production, emphasizes its importance in modelling, spatial analysis, and predicting ecosystem services.

Ecosystem services are essential to present and future generations, and they can be positively influenced by currently implemented management actions. Achieving some

redundancy in the availability of resources for service providers is one possible way to sustain multiple target groups simultaneously. Consequently, ecosystem service delivery and biodiversity can be promoted concomitantly. Finally, research agendas have to integrate the concept that ecosystem services do not act independently, and more research on trade-offs, and synergies has to be carried out.

Author's Contributions

The contribution of Louis Sutter to the data collection, analysis, and publication of the contents in this thesis was as follows:

- In charge of the Swiss case studies for pollination and pest control, comprising elaboration of sampling protocols, organisation of field work, data collection and analysis.
- Consolidation of all data collected in Work package 3: "Actual ecosystem services of semi-natural habitats" from the QuESSA project.
- **Introduction:** author
- **Chapter 2:** contribution to sampling protocols, data collection, preparation, statistical analysis and main author
- **Chapter 3:** contribution to sampling protocols, data collection, preparation, statistical analysis and main author
- **Chapter 4:** designed the whole study, data collection, preparation, statistical analysis and main author
- **Discussion:** author

ZUSAMMENFASSUNG

Die Natur stellt eine Vielzahl an Dienstleistungen für den Menschen zur Verfügung. Beispiele dafür sind die Bestäubung von Nutzpflanzen durch Tiere oder die Kontrolle von Pflanzenschädlingen durch ihre natürlichen Feinde. Diese Funktionen sind als Ökosystemdienstleistungen bekannt und weltweit von entscheidender Bedeutung für die landwirtschaftliche Produktion. Die vorliegende Arbeit untersucht, mittels Feldstudien in Schweizer Agrarlandschaften, das Potenzial der oben genannten Ökosystemdienstleistungen, welche von Insekten erbracht werden sowie deren Wechselwirkungen und Effekte auf den landwirtschaftlichen Ertrag. Sie hat zum Ziel: Erstens, die Ressourcennutzung von verschiedenen Bestäubergilden zu untersuchen, mit der Frage, ob durch eine ökologische Aufwertung von halbnatürlichen Lebensräumen mehrere Komponenten der biologischen Vielfalt gleichzeitig gefördert werden können. Zweitens, die Auswirkungen ökologischer Verbesserungsmassnahmen auf lokaler und regionaler Ebene, auf Ökosystemdienstleistungen und deren mögliche Auswirkungen auf den Ertrag zu evaluieren. Und drittens, zu testen, ob diese Ökosystemdienstleistungen unabhängig oder synergistisch den Ertrag beeinflussen können und den monetären Wert von Insektenbestäubung und Schädlingskontrolle abzuschätzen.

Kapitel 1 untersucht die Beziehung zwischen den verfügbaren Nahrungsressourcen für unterschiedliche Bestäubergilden in halbnatürlichen Lebensräumen sowie deren bevorzugte und proportionale Nutzung. In einer Feldstudie wurden, im Vergleich zur Abundanz, überproportional besuchte Pflanzen – sogenannte Schlüsselpflanzen – von wilden Nutzpflanzenbestäubern, seltenen Bienen und Honigbienen identifiziert. In Übereinstimmung mit der Netzwerktheorie nutzten seltene Bienen eine Teilmenge der Pflanzenarten, welche von den anderen Bestäubergilden besucht wurden; zeigten aber Präferenzen für unterschiedliche Pflanzenarten. Trotz der unterschiedlichen Präferenzen zwischen den verschiedenen Insektengruppen, wurde die Abundanz aller Gruppen gleichmässig positiv durch erhöhte

Pflanzendiversität beeinflusst. Schliesslich prognostizierte die Abundanz von Schlüsselpflanzen und die funktionelle Komplementarität der Pflanzengemeinschaft die Bienenabundanz besser als das totale Blühangebot. Diese Ergebnisse zeigen, dass die Pflanzendiversität von halbnatürlichen Lebensräumen verschiedene Komponenten der biologischen Vielfalt fördern kann. Dies wiederum kann zu positiven Effekten für verschiedene Funktionen, wie Ökosystemdienstleistungen und die Erhaltung der Artenvielfalt, führen.

In **Kapitel 2** wurde die Bestäubung durch Insekten sowie die natürliche Schädlingskontrolle in Abhängigkeit von lokal angesäten ökologischen Vorrangflächen und Landschaftskomplexität gemessen. Sowohl die Bestäubung durch Insekten als auch der Schädlingsfrass stiegen bei erhöhter Landschaftskomplexität um 10% beziehungsweise 13%. Die Zunahme der Bestäubung war in Feldern, welche an eine ökologische Vorrangfläche grenzten stärker als neben einer Ackerkultur. Die Bewirtschaftung der Felder erwies sich als Hauptparameter für die Erklärung des Ertrags. Schädlingsfrass, nicht aber die Bestäubung durch Insekten, verbesserte den Ertrag bei durchschnittlicher Bewirtschaftungsintensität zusätzlich um 9%. Dies führt zur Schlussfolgerung, dass lokales Ansähen von ökologischen Vorrangflächen, vor allem in Kombination mit erhöhter Landschaftskomplexität die untersuchten Ökosystemdienstleistungen fördern kann. Die daraus resultierenden Vorteile können maximiert werden, wenn lokale Habitate und Landschaftskomplexität optimal kombiniert werden. Diese Ergebnisse sollten Landwirte ermutigen, ökologische Vorrangflächen unter Berücksichtigung der Landschaftskonfiguration zu implementieren und zu erhalten.

Die Studie in **Kapitel 3** konzentriert sich auf mögliche Wechselwirkungen zwischen einzelnen Ökosystemdienstleistungen. Bis vor kurzem wurden Ökosystemdienstleistungen vorwiegend singulär, ohne potentielle Wechselwirkungen untereinander zu berücksichtigen, untersucht. Das vorliegende Experiment konnte jedoch starke synergistische Wirkungen von

Insektenbestäubung und simulierter Schädlingskontrolle auf den Ertrag feststellen. In Kombination erhöhte sich der Ertrag um 23%, wobei die einzelnen Ökosystemdienstleistungen 7% beziehungsweise 6% beisteuerten. Die Synergieeffekten betrugen 10%. Der potenzielle wirtschaftliche Nutzen war, durch eine zusätzliche Steigerung der Ertragsqualität, um weitere 12% erhöht. Dieser starke Effekt der Wechselwirkung zwischen zwei Ökosystemdienstleistungen, von zentraler Bedeutung für die globale Produktion von Nahrungsmitteln, unterstreicht die Wichtigkeit deren Berücksichtigung bei Modellierung, räumlicher Auswertung und Vorhersagen.

Ökosystemdienstleistungen sind von zentraler Bedeutung für das Wohlergehen heutiger und zukünftiger Generationen. Die vorliegenden Resultate zeigen nun, dass Ökosystemleistungen und damit der Nutzen natürlicher Ressourcen für den Menschen positiv mit derzeit umgesetzten Bewirtschaftungsmassnahmen beeinflusst werden können. Zusätzliche positive Effekte können erzielt werden, wenn in der Verfügbarkeit von Ressourcen für Nützlinge eine gewisse Redundanz erreicht wird. Dies bietet die Möglichkeit zur gleichzeitigen Förderung mehrerer Zielgruppen, um Ökosystemdienstleistungen und Biodiversität parallel zu fördern. Abschliessend ist es wichtig anzuerkennen, dass Ökosystemdienstleistungen nicht unabhängig voneinander sind und folglich weitergehende Forschung über Kompromisse und Synergien zwischen Ökosystemdienstleistungen unabdingbar ist.

INTRODUCTION

Louis Sutter


Photo M. Tschumi

General introduction

Biodiversity and agricultural intensification

Agriculture has contributed to biodiversity enhancement in earlier centuries (Van Elsen 2000) through the creation of new habitats and breeding practices. Since then agricultural intensification has successfully increased food production, following the steadily increasing demand due to human population growth (Matson 1997). However, the intensification of agricultural production in recent decades has led to a decline and loss of biodiversity (e.g. Robinson & Sutherland 2002). The simplification of agro-ecosystems, through homogenisation and a reduction of landscape diversity, alongside the application of mineral fertiliser and phytosanitary products (Pywell *et al.* 2012) are among the primary underlying factors (Tscharntke *et al.* 2012). This intensification has impacted biodiversity negatively on multiple levels (e.g. Evenson & Gollin 2003) and arthropods in particular have suffered (Desneux, Decourtye & Delpuech 2007). This group relies on resources provided alongside the heavily used agricultural matrix to survive and reproduce in a successful manner. Elements in the landscape that are managed in an animal friendly way – semi-natural habitats – such as hedgerows, flower strips, fallow land or extensively managed meadows, offer supplemental resources which are vital for these populations in agro-ecosystems (Pywell *et al.* 2006; Klein *et al.* 2012), and could potentially mitigate their decline via plant-provided resources such as shelter, suitable microclimates, over-wintering sites and food (Jeanneret *et al.* 2003; Sardiñas & Kremen 2014). The importance of such landscape mediated resource effects on arthropods is relatively well documented in scientific literature (e.g. Shackelford *et al.* 2013). However, decisive key resources for the support of these taxa, the determinants of resource use, and in how far additional resource provision can increase the possibility of inversing biodiversity loss remains unclear.

To increase the amount of available resources for animals on agricultural land various measures have been implemented (Batáry *et al.* 2015). Such mitigation measures target

different animal taxa to provide resources, which are not available elsewhere, with the aim of reducing pressure on populations. The goal of such mitigation measures is to support the development of rural areas and to protect biodiversity (European Union 2013). The protection of biodiversity is justifiable by the intrinsic value of each species, which designates a value to biodiversity independent of its potential usefulness for human beings (Soule 1985). However, the loss of biodiversity is not only an issue regarding its intrinsic value, but also a threat to the provision of crucial ecological functions (Hooper *et al.* 2012).

Ecosystem services: Concept and values

Ecosystem functions with a direct benefit for humans are termed ecosystem services and encompass a large set of goods and functions provided by ecosystems, vital for human well-being (Daily, Naylor & Ehrlich 1997). This concept was originally developed to illustrate the benefits that natural ecosystems generate for society and to raise awareness for biodiversity and ecosystem conservation (Westman 1977). The millennium ecosystem assessment categorised the benefits of ecosystems for humans into four categories: Provisioning services: Managed ecosystems like agricultural land are designed to provide food, forage, fibre, bioenergy, and pharmaceuticals. Supporting services: These comprise functions like soil formation and fertility, cycling of nutrients and water purification. Cultural services: Defined as non-material benefits obtained from ecosystems such as cultural diversity, aesthetic values, cultural heritage, recreation, and ecotourism. Regulating services: Natural ecosystems may also purify water and regulate its flow into agricultural systems, providing sufficient quantities at the appropriate time for plant growth. Traditionally, agro-ecosystems have been considered primarily as sources of provisioning services, but their contributions to other types of ecosystem services are increasingly recognized (MEA 2005). While the global demand for reliable provisioning of ecosystem services is increasing, many of these services are declining due to anthropogenic driven ecosystem changes (Vitousek 1997). Among the multiple provisioning and supporting ecosystem services that contribute to

yield in agro-ecosystems, animal-mediated crop pollination represents a key service with an estimated economic value for global crop production of € 153 billion per year (Gallai *et al.* 2009). At the same time approximately one third of the potential global crop yield is lost to pests (Oerke 2005), crop yield losses, as a result of insect pests, are estimated to likely be no less than 10 % and are stable or increasing worldwide, despite increasing insecticide use (Pimentel & Burgess 2014). Natural control of insect pests is therefore a highly valued ecosystem service (Costanza *et al.* 1997; Losey & Vaughan 2006). Pollination directly increases and stabilizes the yield of ca. 70% of the world's most important crops (Klein *et al.* 2007), whereas natural pest control directly reduces the negative impact of pests on crop plants.

Both pollination and natural pest control are accomplished by mobile, predominately wild animals, although increasing efforts have been made to promote fungi and bacteria as service providers for pest control (Liu *et al.* 2013; Eckard *et al.* 2014), and reduce pollinator dependence of crops through breeding of self-fertile cultivars (Hudewenz *et al.* 2013). Responses of these mobile ecosystem services providers, such as pollinators or pest antagonists, to above mentioned mitigation measures is likely contingent based on the composition of the landscape and the amount, quality and configuration of resources distributed at landscape scale (Scheper *et al.* 2013; Jonsson *et al.* 2015). Improved management of ecological infrastructures can support service providers and contribute to ecosystem service delivery (Tschumi *et al.* 2015). Complex landscapes (i.e. with more structure, smaller patch sizes and large amounts of semi-natural habitats) have been found to support more diverse populations of natural enemies (Bianchi, Booij & Tscharntke 2006), which are positively related to improved service delivery (Letourneau *et al.* 2009; Vergara & Badano 2009). The efficiency or strength of ecosystem services may therefore depend on the landscape composition (Holzschuh *et al.* 2007). However, little is known about potential

interactive effects of local and landscape-wide available resources on the provisioning of multiple ecosystem services.

Considerable effort has been made to quantify, map and identify the drivers and consequences of ecosystem services (Bommarco, Kleijn & Potts 2013), however increasing knowledge on ecosystem services revealed that they rarely act in isolation, but potentially interact with each other. Alterations in shared drivers (e.g. land use- or climate change) can result in synergies or trade-offs between multiple ecosystem services (Bennett *et al.* 2009). Consequently there have been repeated calls for research aimed towards a better understanding of the relationships among multiple ecosystem services, and their underlying mechanisms, to improve effective ecosystem management, maximising ecosystem services in a sustainable way (Seppelt *et al.* 2011). Maximising multiple ecosystem services in agro-ecosystems is crucial to meet the challenge of long-term food security through sustainable crop production, without jeopardizing biodiversity and ecosystem health (Kennedy *et al.* 2013). Ecosystem services delivered by arthropods in agricultural ecosystems represent a public good of paramount importance. However, quantification and detection of synergies and trade-offs between agricultural management and beneficial ecological functions has to be carried out. Investigation into the relationship of available resources for service providing organisms in semi-natural habitats, the strength, and consequences for crop yield of the provided ecosystem services, and the characterisation of the nature of interactions between these measured benefits lie within the objectives of this thesis.

The QuESSA project

This thesis was accomplished within the European research project QuESSA (Quantification of Ecological Services for Sustainable Agriculture, EU FP7, Contract Number 311879). QuESSA emerged in response to the call for new insights and tools that can support high crop production in sustainable crop management systems. In a context of pressure to increase food production, QuESSA explores the ecosystem service potential of semi-natural

habitats and will define management options for semi-natural habitats at farm, regional and European level, aimed at maximising the ecosystem service provisioning of semi-natural habitats. Furthermore the cascading aspects of landscape and management, natural enemies, pest densities and crop damage are addressed in an integrated approach (Bianchi, Booij & Tscharntke 2006). QuESSA takes advantage of the collaborating eight European countries, covering four climatic zones and many farming systems, to quantify effects of semi-natural habitats on ecosystem services in a standardised way, to allow the highest possible knowledge transfer to local stakeholders and future agricultural policymakers.

Study system and methodological approach

The high demand and intensive production of oilseed rape (*Brassica napus* L.) characterise it as a globally relevant crop, ideal for studying the consequences of multiple ecosystem services. Oilseed rape is one of the the most vital food, fodder, and biofuel crops worldwide (Eurostat 2010; FAO 2016). However, many pest species invoke the usage of phytosanitary products in oilseed rape that could potentially be replaced by natural pest control to mitigate yield loss (Alford 2003). Nevertheless, beside harmful effects of pesticide on animals, cases of insect resistance to synthetic pyrethroids have emerged (Derron *et al.* 2004). Therefore, enhancing predation would be a solution to decrease the overall human input. The most severe oilseed rape yield losses in Europe (up to 100% without pest control) are due to herbivory by the pollen beetle, *Meligethes aeneus* Fab. (Coleoptera: Nitidulidae). The adult beetles feed on the pollen of open and closed flowers, the latter leading to flower development abortion and consequently a smaller number of fruits and therefore reduced yield. A series of hymenopteran wasps, along with ground dwelling arthropods, are efficient candidates to provide natural pest control of pollen beetles, but show very large variations in their efficiency (Thies & Tscharntke 1999; Büchi 2002; Alford 2003; Schneider *et al.* 2015). Bumblebees, together with honey bees and a series of solitary bee and hoverfly species are the most abundant flower visitors of oilseed rape in Europe (Garratt *et al.* 2014). Oilseed rape is

considered to mainly be pollinated by wind, because currently grown cultivars with restored fertility are self-fertile. But recent evidence suggests that insect pollination can significantly increase the number of seeds per fruit in commonly grown varieties, with consequences for crop yield (Bommarco, Marini & Vaissière 2012; Hudewenz *et al.* 2013). The economic importance of oilseed rape production, along with the possibility of studying insect pollination and natural pest control within the same system make it a very suitable study system for many agro-ecological questions, with important implications for policy, food production and biodiversity conservation.

Studying biological systems presents a series of challenges, when exploring their functioning. Ecosystem services are often measured under uncontrolled conditions, where many influencing factors such as climate or soil conditions may have effects (Marini *et al.* 2015; Bartomeus, Gagic & Bommarco 2015). Many of these more or less hidden factors are usually measured to determine their importance alongside other explanatory variables and account for uncontrolled variation in statistical models. Unfortunately such studies are rather descriptive and the underlying mechanisms remain difficult to identify (Brennen *et al.* 2002). Although conclusions may sometimes be difficult, studying such patterns at landscape level is necessary because this is the scale where ecosystem services act, investments are realised, policy applies, and where stakeholders thirst for new insights (Daily *et al.* 2009). To gain additional mechanistic insights, one chapter of this thesis presents data from an experiment with manipulated treatments, which allowed identification of mechanisms and the disentanglement of drivers of the emerged patterns. Experimental control is accompanied by a reduced applicability to real world systems, because natural systems have a higher inherent complexity that can seldom be completely reflected in manipulated experiments. Combining descriptive landscape studies and results from manipulative experiments, along with several cutting edge statistical methods, facilitates consideration of their advantages in combination while bearing their limitations in mind, leading to new conclusions.

Study aims

Research on insect pollination and natural pest control in agro-ecosystems has made major improvement over the past decade. Nonetheless, this work aims to close three partially remaining gaps in the current knowledge. To increase and refine current knowledge of the potential of ecosystem services, the aim of this study is to characterise the chain of actions from landscape parameters in agro-ecosystems, over service providing organisms and their used resources to ecosystem services as valuable contributions to crop yield. More specifically the aims are as follows: (i) To determine differences in resource provision by herbaceous semi-natural habitats in agro-ecosystems for diverging target groups of pollinators, increasing the understanding of positive effects of improved plant species richness on different conservation target groups, and their consequences for biodiversity conservation and ecosystem services. (ii) To evaluate the effects of local and landscape wide ecological enhancement measures on pollination by insects and natural pest control and their influence on crop yield alongside local management factors. (iii) To quantify the relative importance of insect pollination and pest control, and in particular, their interactive effects – the relationship among ecosystem services – on yield, resulting in an estimation of the potential economic value of these effects.

CHAPTER 1

Enhancing plant diversity in agricultural landscapes promotes both rare and crop-pollinating bees through complementary increase in key floral resources

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Manuscript formatted for and submitted to *Journal of Applied Ecology*


Photo M. Tschumi

Enhancing plant diversity in agricultural landscapes promotes both rare and crop-pollinating bees through complementary increase in key floral resources

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Abstract

1. Enhancing key floral resources is essential to effectively mitigate the loss of pollinator diversity and associated provisioning of pollination functions in agro-ecosystems. However, effective floral provisioning measures may diverge among different pollinator conservation targets, such as the conservation of rare species or the promotion of economically important crop pollinators. We examined to what extent and how such diverging mitigation goals could be reconciled.
2. We analysed plant–bee visitation networks of 64 herbaceous semi-natural habitats representing a gradient of plant species richness to identify key resource plants of rare bees and crop-pollinating wild and managed bees (i.e. honey bees).
3. Considering overall flower visitation, the mostly generalist rare bees tended to visit nested subsets of resource species also visited by dominant crop pollinators (46% and 77% nestedness explaining visitation similarity compared with wild crop pollinators and honey bees, respectively). However, the set of preferred key plant species (i.e. species disproportionally more visited than expected according to their floral abundance) was considerably more distinct among bee target groups.
4. Flower visits of all bee target groups increased with plant species richness at a similar rate. Our analyses revealed that an exponential increase in the flower abundance of the identified key plant species and plant functional complementarity ─ rather than total flower abundance ─ were the key determinants of these relationships.
5. **Synthesis and applications.** We conclude that the multiple goals of preserving high bee diversity, conserving rare species and sustaining dominant crop pollinators can be reconciled if mitigation measures ensure high complementarity of key floral resources for different pollinator target groups. Our findings highlight the importance of identifying and promoting such plant species for pollinator conservation measures in agricultural landscapes.

Keywords: agri-environment schemes, multiple ecosystem functioning, endangered species, animal-mediated pollination, ecological focus areas, grassland extensification, nestedness, pollinator conservation, resource use, wild flower strips,

Introduction

Concerns over the loss of biodiversity and impaired functioning and provisioning of ecosystem services in agro-ecosystems have triggered the implementation of a suite of agri-environmental measures to mitigate these negative consequences of conventional agricultural intensification (MEA 2005). The implicit or explicit goals of such agri-environmental measures are to contribute to multifunctional agro-ecosystems (Wratten *et al.* 2012), including the promotion of multiple ecosystem services to sustain crop production (Bommarco, Kleijn & Potts 2013), while conserving farmland biodiversity and protecting rare and endangered species (Anonymous 2005). However, multiple components or aspects of biodiversity may require distinct objectives and mitigation approaches to be effectively managed, since important life-history traits may vary considerably among different mitigation target groups (Kleijn *et al.* 2011; Korpela *et al.* 2013; Ekroos *et al.* 2014). Key questions are to what extent it might be possible to reconcile the potentially diverging goals of rare species protection, biodiversity conservation, and provision of ecosystem services with the same habitat management measures, and what the critical determinants of managed habitats are that drive effective promotion of multiple biodiversity target groups.

Pollinators and bees in particular represent an important component of agro-ecosystems' biodiversity and appear to be particularly suitable to address these questions. Bees (Apoidea) are a species-rich taxonomic group reflecting a broad variety of life-history traits; they rely to differing degrees on specific floral and nesting resources, making them sensitive indicators of the response of overall biodiversity to habitat loss and degradation, and of the success of ecological enhancement measures (Tscharntke, Gathmann & Steffan-Dewenter

1998; Scheper *et al.* 2013). Bees also provide vital pollination services to wild plants (Ollerton, Winfree & Tarrant 2011) and crops (Klein *et al.* 2007; Garibaldi *et al.* 2013) and are therefore of paramount ecological and economic importance (Gallai *et al.* 2009). However, several studies have reported strong declines of both managed (Potts *et al.* 2010) and wild bee populations, as well as bee diversity, during the last decades (Biesmeijer *et al.* 2006; Carvalheiro *et al.* 2013). Crop pollination services have often been used as an argument to conserve and restore pollinator diversity, but only a restricted number of wild pollinator are considered of substantial value for crop pollination along with managed bees (Kleijn *et al.* 2015). It has been shown that these wild crop pollinators are, at least currently, usually the most abundant bee species in agro-ecosystems and seem to be more resilient to land use and other anthropogenic changes (Rader *et al.* 2014; Kleijn *et al.* 2015). Habitat management focusing exclusively on crop pollinators and crop pollination services may therefore pose a serious problem to pollinator biodiversity and rare species conservation if these different target groups should indeed exhibit different habitat (management) requirements (Senapathi *et al.* 2015a). A better understanding of the divergent or overlapping resource requirements among these different target groups is crucial for (cost-) effective measures aimed at conserving pollinator biodiversity, pollination services or both.

Loss of floral resources is considered as one of the main drivers of bee decline (Scheper *et al.* 2014), and floral resource (pollen and nectar) provisioning is accordingly considered decisive in habitat management for both wild and managed bees (Dicks, Showler & Sutherland 2010; Scheper *et al.* 2014). Thus, it is crucial to inform management with knowledge on which floral resource plant species are particularly important to sustain different bee target groups, i.e. (i) wild crop pollinators, (ii) managed crop pollinators and (iii) rare bee species, and to what extent these resources are complementary or overlapping among target groups. Such knowledge requires quantitative data on the floral resource use of bees e.g. through the collection of plant–pollinator networks. Indeed, recent advances in our

understanding of the architecture of such plant–pollinator networks and underlying drivers allow testing network-theoretical predictions on observed flower visitation patterns. Plant–pollinator and other mutualistic networks tend to be nested and asymmetrical, such that rare species mainly interact with common species, and common species with both common and rare species (Bascompte & Jordano 2007). Based on this prediction, we would expect to find rare bees and common bees to use to a large extent the same, common resource plant species, implying that all target groups could be sustained with similar plant communities and mitigation measures. Indeed, rare bees may visit a subset plant species as common crop pollinators simply because these plants are the ones most abundantly flowering. However, preference for a floral resource plant species could be a decisive measure of its importance for habitat restoration measures. In fact, it is likely that preference for such key plants for different target groups is masked by density-dependent visitation (Russo *et al.* 2013), and that preferred floral resource species are clearly more distinct among target groups, with important implications for effective bee conservation. However, to our knowledge, these predictions have not yet been explored in real-world agricultural landscapes.

In order to better target and improve the effectiveness of agri-environmental measures, such as grassland extensification or the improvement of field margins, regarding pollinator conservation, in addition to potential other goals, it is important to better understand to what extent the availability resources for specific bee target groups are enhanced by such measures. A common goal of many agri-environment measures to improve the ecological quality of grasslands and other semi-natural habitats in agricultural landscapes is to enhance plant species diversity, which is also used as a benchmark for the success of measures (Kleijn *et al.* 2006). Although not always, many schemes achieve this goal (Albrecht *et al.* 2007; Aviron *et al.* 2009). Increased herbaceous plant species richness in such schemes have generally been found to be also positively associated with increased richness of bee and other pollinator species (Albrecht *et al.* 2007; Scheper *et al.* 2013). Indeed, total local floral resource

abundance is, in addition to landscape context, considered as a key driver of the effectiveness of mitigation measures to enhance bee densities and potentially associated pollination services (Scheper *et al.* 2015). However, since no direct flower visitation observations have usually been carried out in such studies, it is not clear which subsets of floral resource species are actually used or preferred by different bee target groups, and whether flower abundance of these key plants may actually better predict the success of mitigation measures, rather than total species richness or flower abundance. In conclusion, there is a strong need for a better understanding of the relationships of the floral abundance of key resource plant species for bee target groups with local plant species richness and flower abundance, as well as the relative importance of these different predictors sustaining bees across target groups. Such knowledge is crucial for improving the effectiveness of mitigation measures with respect to different conservation targets, and thus to assess how habitat management may simultaneously protect rare bees, bee diversity and dominant crop pollinating bees. In the present study, we therefore addressed the following specific aims:

1. Identify key resource plant species of herbaceous semi-natural habitats for both rare and dominant crop-pollinating bees.
2. Test the prediction of plant–pollinator network theory stipulating that plants visited by rare bee species are a subset of plants visited by common crop-pollinating bees.
3. Test the hypothesis that multiple target groups of pollinator conservation, i.e. rare and dominant crop pollinating bees, can be simultaneously promoted by plant species–rich herbaceous semi-natural habitats.
4. Identify the underlying key drivers of such relationships, in particular to determine the importance of key floral resource abundance and resource complementarity in plant species–rich herbaceous semi-natural habitats.

Materials and Methods

Study area and sampling design

The study was conducted in 2013 and 2014 in agricultural landscapes of the northern part of the central Swiss plateau (cantons Zurich and Aargau) characterized by a small-scaled mosaic of permanent herbaceous vegetation, mainly grasslands of various management intensity, arable crops, and forest remnants. A set of eight different landscape sectors (3 km radius, smallest distance between midpoints 6.75 km) were selected along a gradient of proportion of non-crop herbaceous vegetation and other semi-natural habitats estimated from satellite images. This focus was chosen because the food and nesting resources provided by these habitats are considered to be of critical importance for the persistence of bees and other insects in agricultural landscapes (Shackelford *et al.* 2013). The major types of non-crop herbaceous vegetation in the study region were: (1) areal permanent grassland, mainly meadows, conventionally or extensively managed according to the prescriptions of the Swiss agri-environment scheme (Bundesrat 2015), (2) naturally colonized or sown field margins and grassy strips established between arable crops, (3) herbaceous strips along hedgerows and (4) herbaceous strips along forest edges. Two distinct patches of each of the four herbaceous semi-natural habitat types (hereafter habitat elements) were chosen within each landscape sector (64 habitat elements in total), such that all sampled habitat elements were at least 200 m apart from each other. The habitat elements in the eight selected landscape sectors covered a plant species richness gradient of 46 to 68 species, which was significantly positively correlated (Pearson correlation coefficient = 0.80) with the proportion of sampled habitat elements, managed according to the prescriptions of the Swiss agri-environment scheme (Bundesrat 2015).

Sampling of plant–pollinator interactions

Plant–bee visitation networks were recorded using standardized transect walks (Gibson *et al.* 2011): in each of the eight habitat elements in all sectors, 50 m belt transects of a width of 1.5 m were walked during a maximum of 10 minutes per transect at a constant pace while recording all individual bees visiting flowers (i.e. contacting flower reproductive organs). To account for their larger spatial extent and heterogeneity in the distribution of flowering plants and flower-visiting bees, two 50 m transects were walked in herbaceous habitat elements wider than 3 m, whereas only one 50 m transect was walked for narrow habitat elements with a width of ≤3 m. Standardized transect walks were performed in each of the 64 habitat elements during four sampling rounds distributed over the entire vegetative growing season between May 2013 and April 2014. This sampling scheme resulted in a total observation time of 64 hours. The order and time of day when different habitat elements and landscape sectors were sampled varied between sampling times to avoid confounding of daytime and habitat element or sector. Observations were done between 0930 and 1730 hours with good weather conditions (temperature above 13 °C with at least 60% clear sky and no wind) according to Pollard & Yates (1993). Whenever possible, flower-visiting bees (Apoidea) and visited plants were identified in the field to species level, or, if this was not possible, bees and plants were collected and identified to species level in the laboratory. Time was stopped for the duration of insect handling (catching and transfer to killing jar).

Classification of bees into target groups

The classification of bees as dominant crop pollinators follows Kleijn et al. (2015), considering bee species classified as dominant crop pollinators for central Europe also to be important crop pollinators for the study region (see Table S1 in Supporting Information S1). Due to the high density of the western honey bee (*Apis mellifera* [L.], hereafter honey bee) in the study region, and because it is a managed pollinator species in the study region, honey bees and wild crop pollinators were distinguished in the analyses. Flower-visiting bees were

classified as ‘rare’ according to the red list for bees of Switzerland (Amiet 1994), considering all species classified as ‘critically endangered’, ‘endangered’ or ‘vulnerable’ (Table S2).

Assessing floral abundance

During each of four flower visitation sampling rounds, floral abundance was quantified in 10 individual plots (1 × 1 m) along the belt transects immediately after the transect walks. Number and type of inflorescence of each flowering plant species were recorded. Floral abundance of each species was then calculated as the total floral area as follows: for species with circular flower morphologies (individual flower, flower head, corolla, corymb, umbel) diameter or radius was converted to the area of a circle; for other flower morphologies (spadix, cyme, flowered stem, capitulum, panicle, raceme, spike), the flowering surface was derived as the surface of a cylinder. Inflorescence dimensions were compiled from the following sources: eFloras (Brach 2015), The NSW Plant Information Network System (Royal Botanic Gardens and Domain Trust 2016), Naturegate (NatureGate Promotions 2016), E-Flora BC: Electronic Atlas of the Plants of British Columbia (Klinkenberg 2015), and Pignatti (1982).

Statistical analysis

To identify important floral resource plant species that are frequently visited by the different bee target groups, all visited plant species were ranked according to their number of visits received by bees belonging to different target groups summed over the four sampling periods (Table S3). In a further step, we identified plant species disproportionally more frequently visited than expected according to their floral abundance (key plant species; objective 1): for each bee target group, a generalised linear mixed-effects model (lme4::glmer.nb; Bates *et al.* 2014) with flower abundance as explanatory and number of visits per plant species in a landscape sector as response variable was fitted. To account for habitat elements being nested in landscape sectors, sector was included as a random factor. Species

above the 95% confidence interval of the significant linear flower abundance–bee visit relationship were identified as 'key plant species' (Russo et al. 2013).

To determine how similar (overlapping) or dissimilar (complementary), respectively, the different bee target groups were in their overall and preferred use of resource plants, dissimilarity was calculated for each pairwise bee target group comparison using Jaccard and Bray–Curtis dissimilarity. While Jaccard dissimilarity is based on presence–absence data and thus most suitable to detect differences among bee target groups at plant species level, Bray–Curtis dissimilarity also considers differences in the proportion of visits and thus different floral resource use. To further address objective 2, nestedness components of Jaccard dissimilarity were calculated with 'betapart' (Baselga & Orme 2012). This method allows quantifying the nestedness and turnover components of between-group beta-diversity of communities.

To address objective 3, the explanatory variables 'total plant species richness', 'bee target group' and their interaction were fitted in separate models with the response variables: (1) total number of present key plant species per landscape sector and bee target group, (2) flower abundance of key plant species per landscape sector and bee target group and (3) number of visits per landscape sector and bee target group. For (1), distribution of residuals was normal, whereas generalised linear models with negative binomial error distribution (MASS::glm.nb; Venables & Ripley 2002) were used for (2) and (3) to account for overdispersion in the residuals when assuming Poisson errors. For all models, assumptions were checked according to the graphical validation procedures recommended by Zuur et al. (2009).

To address objective 4, automated model selection based on Akaike's information criterion for small samples sizes (AICc) was performed (MuMin::dredge; Barton 2009). Linear models with flower visits as response variable and total flower abundance, total plant species richness, flower abundance of key plants, richness of key plant species and plant

functional complementarity as explanatory variables were fitted for multimodel inference. Functional complementarity is a community-level measure of ecological niche complementarity (Blüthgen & Klein 2011) and was calculated as the total branch length of a functional dendrogram based on differences in flower visitor assemblages between plant species (Devoto *et al.* 2012). Relative importance of variables is defined as the proportion of models in which a parameter is present, within the top-n models with delta AICc ≤ 5 compared to the best model. Although flower abundance of key species and total plant species richness were significantly correlated (Table S4), removing one variable did hardly change the relative importance of the other, and as the model was not used for statistical inference or quantitative predictions, but to assess the relative importance of explanatory variables, both parameters were included in the set of candidate models. All statistical analyses were performed in R 3.2.3 (R Core Team 2015).

Results

Flower visits of bee target groups

We recorded 3,507 flower visits by 69 bee species. Honey bees accomplished 2,277 visits on 56 plant species, whereas wild crop pollinators (21 species, Table S1) visited 64 plant species with totally 925 visits. Eighty-six visits from rare species (18 species, Table S2) were recorded on 34 plant species (Fig. 1a).

Identifying key plant species for bee target groups

All visited plant species are ranked in Table S3 according to their proportional number of visits received by the three bee target groups. Out of the 56 and 64 plant species visited by honey bees and wild crop pollinators, respectively, 10 non-identical plant species were identified as being disproportionally visited by each bee target group, whereas 6 out of the 34 plant species visited by rare bees received more visits than expected given their floral abundance (Fig. 1b, Table S3).

Overlap and complementarity in flower visitation among bee target groups

Complementarity was consistently higher and overlap lower among bee target groups for overall flower visitation than flower visitation of identified key resource plant species: both Jaccard and Bray–Curtis dissimilarity increased by 22% to 48% (Table 1). Rare bees tended to visit a subset of plant species visited by the two other bee target groups, indicated by a relatively high nestedness component of 47% in visitation patterns of rare bees compared with honey bees and in particular with wild crop pollinators (78%) when analysing overall flower visitation (Table 1). Nestedness in flower visitation of honey bees and wild crop pollinators was much lower (17%). However, nestedness in visitation patterns between bee target groups decreased strongly when considering visitation to key plant species, ranging from 0% (honey bees and wild crop pollinators) to 33% (rare species and wild crop pollinators) (Table 1).

Relationships between increased plant species richness, availability of key flower resources and flower visitation

Key plant species richness increased linearly and key plant flower abundance even exponentially with increasing total plant species richness (Table 2, Fig. 2a). The slopes of these relationships were not significantly different among bee target groups (Table 2). Similarly, the number of flower visits by all bee target groups increased with plant species richness at a similar rate, indicated by a non-significant interaction among bee target group and plant species richness (Table 2, Fig. 2b).

Importance of key plants and functional complementarity

Bee target group had the highest relative importance (1.0) as it was present in all 14 best models with delta AICc ≤ 5, followed by functional complementarity of plant species (relative importance 0.86), flower abundance of key plant species and its interaction with bee target group (relative importance of 0.65 and 0.29). Total plant species richness, key plant species richness and total flower abundance had lower relative importance (0.11, 0.08 and 0.07, respectively).

Discussion

Identifying key resource plants for rare bees and wild crop pollinators

The analysis of plant-bee visitation networks revealed plant species which were visited by bees of all target groups, highlighting their particular suitability as resource species in multi-target pollinator mitigation measures. For example, *Origanum vulgare* and *Achillea millefolium* were identified as key plants for all bee target groups. The latter species has also been identified as a suitable food plant for hover flies, which can be important pollinators and pest control agents in agro-ecosystems (van Rijn & Wäckers 2015). Furthermore frequently visited plant species – both proportionally and disproportionally – were *Trifolium* species. Wild bees – both crop pollinating and rare – showed preferences for *T. pratense*, whereas honey bees preferentially visited *T. repens.* These findings are in a line with earlier studies which identified *Trifolium* species as key food resources for bees, particularly as a pollen resource for long-tongued bumblebees (Goulson *et al.* 2005), recommending the inclusion of *Trifolium* species for pollinator mitigating measures (Pywell *et al.* 2006; Decourtye *et al.* 2010). Another Fabaceae – *Melilotus albus* – was preferentially used by just honey bees and therefore represents a plant species which is not optimal for wild bee conservation. Common crop-pollinating but not rare bees preferred additional plant species such as *Centaurea jacea* and *C. scabiosa*, which mainly occur in extensively managed meadows and field margins in the study region.

Higher dissimilarity amongst preferred plant species than overall visited plant species

The nested architecture of mutualistic networks suggests that rare and common bee species should to a large extent use the same abundantly flowering resource plants (e.g. Bascompte & Jordano 2007). Thus, we could expect that the promotion of both rare and common crop pollinating bees should be possible with the same suite of abundantly flowering plant species. This is also predicted by optimal foraging theory, implying flower density-dependent foraging for generalist flower visitors (Russo *et al.* 2013). In our study, this prediction was however only partially confirmed: although rare species indeed visited a subset of plant species

also frequently visited by common bees, the preferred suites of key resource plants used by the different target groups were quite distinct, highlighted by a markedly increased dissimilarity when comparing absolute visitation frequencies with preferential flower visitation. Indeed, 27% of all visited plant species were visited by bees of all target groups, but only 11% of plant species were also preferred by all the target groups. Interestingly, not only did rare and crop-pollinating bees show such complementarity in floral resource preference, but even more wild crop-pollinating bees and honey bees. This highlights the importance of setting clear targets in pollinator conservation, which also should include the separation of honey bees and wild bees when designing and implementing pollinator mitigation measures (Senapathi *et al.* 2015a; Kleijn *et al.* 2015). One explanation for this pattern could be differences in morphological traits leading to different trait-matching, and thus reduced preference (or exclusion) for certain flower morphologies (e.g. *T. pratense* or *Lotus corniculatus* preferred by wild bees but not honey bees). In conclusion, rare bee species indeed use a subset of plant species also used by common crop-pollinating bees, and may therefore profit to some extent from the same floral enhancement measures. However, dissimilar resource preference patterns suggest that this provision is rather achieved through enhanced floral resource complementarity of simultaneously promoted key plant species than through nested resource preference. Our findings highlight the need for a clear distinction between frequently visited and preferred resource plant species when exploring the suitability and relative importance of food plants for pollinator mitigation measures.

Importance of floral abundance of key species and plant functional complementarity for sustaining multiple bee target groups

The importance of setting explicit targets to increase the effectiveness of mitigation measures and to clearly distinguish between pollinator diversity conservation and fostering important pollination services to crops has been recognized (Senapathi *et al.* 2015a; Kleijn *et al.* 2015). However, we still lack a clear mechanistic understanding of key factors driving possible win-win relationships or trade-offs (Ekroos *et al.* 2014). Positive plant diversity-

pollinator diversity relationships are expected and have been repeatedly reported in evaluations of the effects of agri-environment schemes on pollinators (Albrecht *et al.* 2007; Wood, Holland & Goulson 2016). Yet, the slope of this relationship may differ for different target groups: rare bee species may be more specialized on floral resource plants that have become particularly rare in modern intensively managed agricultural landscapes (Scheper *et al.* 2014). Common dominant crop-pollinating bees are, in contrast usually considered to be opportunistic generalists, relying on high densities of floral resources rather than on particularly plant-species rich habitats (Kleijn *et al.* 2015). However, we found strong increases in flower visitation by all three target groups (including wild crop-pollinators and honey bees) with plant species richness, with similar slopes in the relationships across target groups. These results can be well explained by the key finding that the abundance of preferred key floral resources is the critical driver across all bee target groups, together with the detected exponential increase in floral abundance of these key plants with increasing plant species richness. Our findings suggest that floral resource complementarity among plant species is an important mechanistic pathway, driving the success of measures aimed at both pollinator diversity conservation and the promotion of important service providers. Moreover, they indicate that an increase of key floral resources for the different bee target groups, rather than total flower abundance or plant species richness *per se* accounted for the observed positive effect of diverse plant communities on bee visitation. These results have to be taken into account when implementing mitigation measures targeting bees, because they imply that a subset of particularly important flowering plant species can determine the success of mitigation measures.

The strong divergence in key resource plant preference for the different bee target groups suggests that floral resource provisioning for multiple target groups may be most profitable when integrating distinct plant communities of different habitats at landscape levels. Many key resource species are indicators of low nitrogen input and late mowing and are therefore characteristic of extensively managed grasslands (e.g. *Knautia arvensis*), while others are

typical pioneer species found in ruderal and highly disturbed habitats (e.g. *E. vulgare*). Further species such as *O. vulgare* – preferred by all target groups – mostly occur in sown wild-flower strips or enhanced field margins within the study region. This results supports the idea that beyond increasing plant functional diversity and resource complementarity through local habitat management, it is important to sustain different bee target groups and pollinator diversity, restoring habitat diversity and heterogeneity at the landscape scale is also critical (Benton, Vickery & Wilson 2003).

In currently available plant-pollinator networks, sampling completeness is rarely perfect (Chacoff *et al.* 2012). Although we observed 22% of all red list bee species potentially occurring in the study region, it is inevitable that some interactions between scarcely distributed species were missed. However, through sampling all major types of herbaceous semi-natural vegetation in 64 sites, this study can be considered to have high sampling thoroughness. Potential under-sampling of particularly rare bees, which preferably visit scarcely occurring plant species, could have resulted in a slight underestimation of the degree of dissimilarity in floral resource use. However, the diet breadth of the red list species sampled does not support this hypothesis: although some of the rare species sampled are oligolectic (Table S2), none of them are specialised on just one or a few plant species occurring in the study region. Temporal dynamics and continuity in the availability of resources is a potentially important aspect especially for colony-building social bees with long activity periods, such as bumblebees or honey bees (Schellhorn, Gagic & Bommarco 2015). These issues have been the focus of previous studies (e.g. Russo et al. 2013) and were not addressed here. Nevertheless, flower abundance and visitation was sampled throughout the entire flowering period and our conclusions are therefore not limited to specific phenological period but are of general relevance for pollinator conservation regardless of temporal dynamics.

Conclusions and management implications

Setting clear targets in pollinator diversity conservation and restoration schemes, such as mitigating the loss of biodiversity and rare species, ecosystem services, or both, and identifying the key factors driving the effectiveness of measures with respect to these different targets is crucial for their success. In this study we identified the preferred key herbaceous floral resource plants in agricultural landscapes for the important pollinator target groups; rare bees, wild crop-pollinating bees and managed honey bees. We show that although different bee target groups overlap considerably in the plant species they visit, they clearly prefer a distinct of sets of species, which has important implications for mitigation measures. We propose that these preferred key plant species in particular should receive special attention in agri-environmental and other mitigation measures, which aim to promote floral resource provisioning for the different target groups, by targeting habitat management according to the needs of these species, or by including them in seed mixtures for the ecological improvement of grassland. Our findings show that measures incorporated into Swiss agri-environment schemes in agricultural landscapes promote flowering plant species diversity, and in particular the floral resource availability of key species for the different bee target groups. Most agri-environment schemes and other mitigation measures in agricultural landscapes have multiple targets, and these often implicitly include biodiversity conservation and ecosystem service provisioning. Our results suggest that through focusing on floral resource provisioning for rare pollinator species, pollinator diversity and important crop-pollination providers, these multiple goals can be achieved simultaneously, if plant functional complementarity is sufficiently high facilitating the availability of preferred key floral resources of the different target groups. Our study highlights that simply increasing the total quantity of floral resources is not necessarily an effective strategy to achieve specific or multiple pollinator or pollination mitigation targets, but instead careful identification of the resource needs of specific target groups is critical for successful pollinator and pollination conservation.

Acknowledgments

We thank Stephan Bosshart, Bärbel Koch, Matthias Tschumi, Gisela Lüscher and Nina Richner for their help with the fieldwork and Sonja Gerber and Andreas Müller for the identification of wild bees. Protocols were developed jointly with the QuESSA (FP7 grant 311879) project partners. The work could not have been carried out without the support of farmers who graciously let us work on their properties. We are grateful to Jochen Fründ, Felix Herzog, Owen Petchey and Bernhard Schmid for valuable discussions and helpful comments on an earlier version of the manuscript.

Data accessibility

All data associated with this manuscript will be available at the Dryad Digital Repository upon acceptance of this manuscript.

Tables

Table 1 Dissimilarity of plant species community visited by bee target groups. Jaccard dissimilarity (Jaccard), based on presence and absence calculated for each between-group comparison; proportion of nestedness within this dissimilarity (nestedness) based on Baselga & Orme (2012); and Bray–Curtis dissimilarity based on number of visits (Bray–Curtis). All results are shown for all plants visited by bee target groups (left) and only for visited key plants (right). Bee target groups are 'wild crop pollinators' (wcp), 'honey bees' (hb) and 'rare bees' (rare).

	all plants visited			key plants visited		
	Jaccard	nestedness	Bray–Curtis	Jaccard	nestedness	Bray–Curtis
wcp : hb	0.31	17.21	0.514	0.60	0.00	0.680
rare : hb	0.44	46.63	0.510	0.63	20.00	0.693
rare : wcp	0.39	77.50	0.369	0.50	33.33	0.526

Table 2 Results of final models after removing non-significant explanatory variables. F- and log-likelihood-ratio tests (LRT) with shown denominator degrees of freedom (df), sum of squares (SS) or difference in log-likelihood and *P* values from χ^2- or F-test. Significant *P* values ($P < 0.05$) are shown in bold (see Materials & Methods section for detailed description of explanatory variables, response variables and statistical models)

Response variable	Explanatory variables	df	SS	LRT	*P* value
key plant richness	bee target group : total plant species richness	2	6.23		0.077
	bee target group	2	11.08		**0.029**
	total plant species richness	1	38.34		**<0.001**
flower abundance of key plants	bee target group : total plant species richness	2		0.32	0.850
	bee target group	2		2.10	0.348
	total plant species richness	1		53.84	**<0.001**
number of visits	bee target group : total plant species richness	2		1.40	0.495
	bee target group	2		239.43	**<0.001**
	total plant species richness	1		10.02	**0.001**

Figure 1

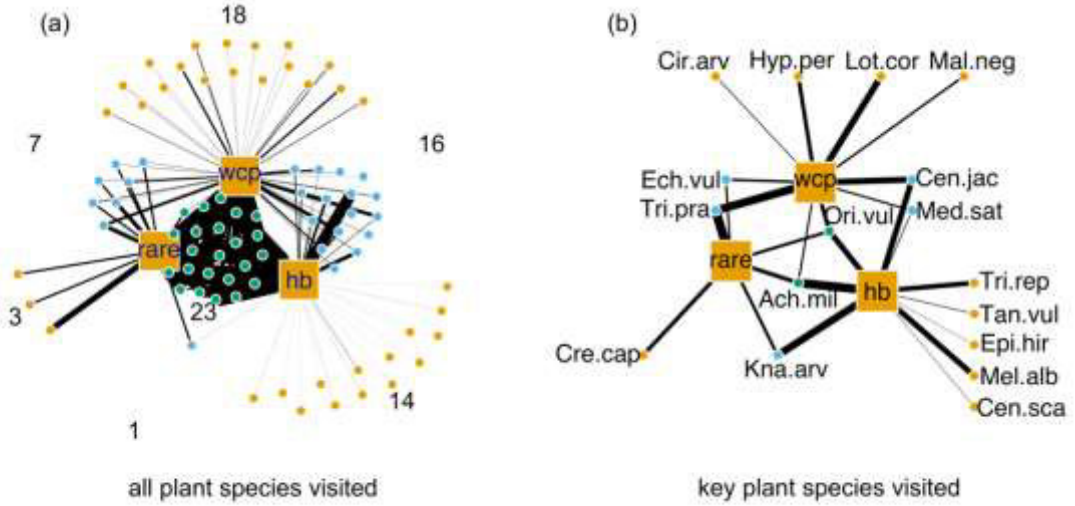

Figure 1 Differential visitation of bee target groups to plants in herbaceous vegetation. (a) Interactions of bee target groups 'honey bees' (hb), 'wild crop pollinators' (wcp) and 'rare bees' (rare) with all visited plant species. (b) Interactions of bee target groups with disproportionally visited key species (complete scientific names of key species are given in Table S3). Width of vertices display the proportional importance of the plants for the visits of a given bee target group. Circles represent plant species (colour = number of interaction partners: orange = 1, blue = 2 and green = 3).

Figure 2

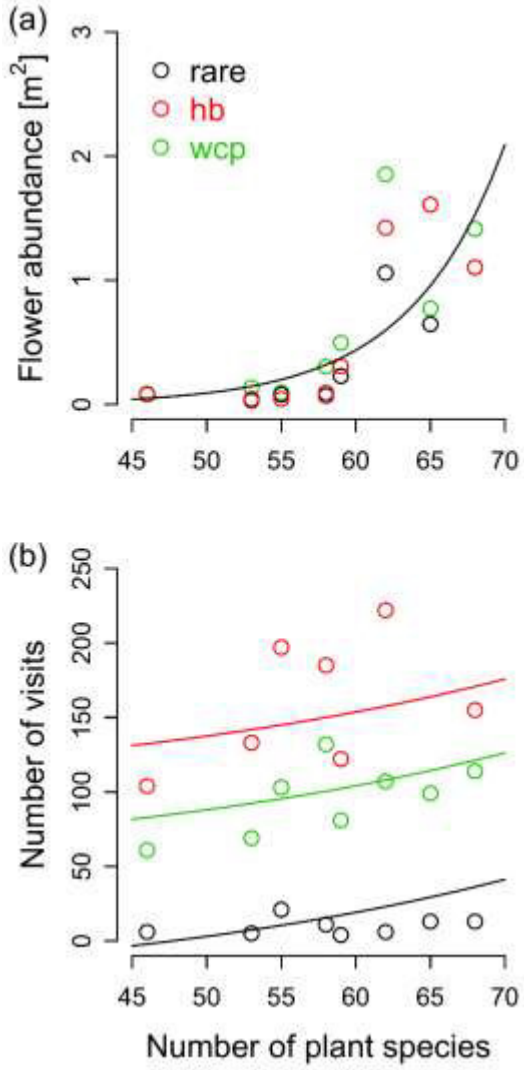

Figure 2 Effect of the plant species richness on (a) flower abundance of key plant species, (b) number of visits per bee target group in each sector. Bee target groups are 'honey bees' (hb, red), 'wild crop pollinators' (wcp, green) and 'rare' bees (rare, black). One value of honey bee visitation (65 plant species, 564 visits) is not displayed on the graph. Shown are data points from all eight sectors and regression lines from linear models for all groups in different colours where between-group difference occurred.

Supporting Information

Table S1 List of wild crop-pollinating bees from Europe that were sampled

Table S2 List of endangered bee species with their conservation status and diet breadth

Table S3 List of all plant species visited by three bee target groups

Table S4 Correlation table of parameters of multimodel inference for relative importance

Table S1 List of wild crop pollinating bees from Europe according to Kleijn *et al.* (2015) that were sampled in the study

nr	species
1	*Andrena carantonica*
2	*Andrena chrysosceles*
3	*Andrena cineraria*
4	*Andrena dorsata*
5	*Andrena flavipes*
6	*Andrena haemorrhoa*
7	*Andrena helvola*
8	*Andrena nitida*
9	*Andrena ovatula*
10	*Andrena subopaca*
11	*Bombus hortorum*
12	*Bombus lapidarius*
13	*Bombus pascuorum*
14	*Bombus pratorum*
15	*Bombus terrestris*
16	*Halictus rubicundus*
17	*Halictus scabiosae*
18	*Halictus simplex*
19	*Lasioglossum malachurum*
20	*Lasioglossum pauxillum*
21	*Lasioglossum politum*

Table S2 List of endangered bee species with their conservation status according to Amiet (1994) and diet breadth according to Westrich (1989). Two wild bee species (*Andrena cineraria* (L.) and *Halictus scabiosae* (Rossi), Tables S1 and S2) detected in our surveys are red listed for Switzerland while at the same time considered as dominant crop pollinator according to Kleijn et al. (2015). As the number of visits of these two species were low in this study, and to avoid double counts, they were not considered as dominant crop pollinators for the study region and the two species were therefore classified as 'rare'.

number	species	conservation status	diet breadth
1	*Andrena cineraria*	vulnerable	polylectic
2	*Andrena hattorfiana*	vulnerable	oligolectic
3	*Andrena lathyri*	vulnerable	oligolectic
4	*Andrena pandellei*	endangered	oligolectic
5	*Andrena viridescens*	vulnerable	oligolectic
6	*Bombus humilis*	vulnerable	polylectic
7	*Bombus sylvarum*	vulnerable	polylectic
8	*Colletes cunicularius*	endangered	oligolectic
9	*Colletes similis*	vulnerable	oligolectic
10	*Halictus scabiosae*	vulnerable	polylectic
11	*Halictus subauratus*	vulnerable	polylectic
12	*Lasioglossum glabriusculum*	vulnerable	polylectic
13	*Lasioglossum lativentre*	vulnerable	polylectic
14	*Lasioglossum marginatum*	vulnerable	polylectic
15	*Lasioglossum nigripes*	vulnerable	polylectic
16	*Lasioglossum pallens*	vulnerable	polylectic
17	*Lasioglossum parvulum*	vulnerable	polylectic
18	*Melitta nigricans*	endangered	oligolectic

Table S3 List of all plant species visited by three bee target groups with disproportionally visited plan species highlighted for each group.

Bee target group	plant species	proportional visits
managed crop pollinators	*Taraxacum officinale*	13.4
managed crop pollinators	*Achillea millefolium*	11.7
managed crop pollinators	*Knautia arvensis*	9.91
managed crop pollinators	*Centaurea jacea*	7.71
managed crop pollinators	*Melilotus albus*	7.53
managed crop pollinators	*Origanum vulgare*	7.43
managed crop pollinators	*Trifolium repens*	6.42
managed crop pollinators	*Crepis capillaris*	6.15
managed crop pollinators	*Leucanthemum vulgare*	3.17
managed crop pollinators	*Trifolium pratense*	3.12
managed crop pollinators	*Melilotus officinalis*	2.57
managed crop pollinators	*Plantago lanceolata*	2.07
managed crop pollinators	*Rhinanthus glaber*	1.88
managed crop pollinators	*Malva moschata*	1.79
managed crop pollinators	*Erigeron annuus*	1.42
managed crop pollinators	*Medicago sativa*	1.33
managed crop pollinators	*Rhinanthus alectorolophus*	1.24
managed crop pollinators	*Lotus corniculatus*	1.19
managed crop pollinators	*Tanacetum vulgare*	1.1
managed crop pollinators	*Vicia sepium*	0.92
managed crop pollinators	*Silene flos cuculi*	0.73
managed crop pollinators	*Daucus carota*	0.73
managed crop pollinators	*Epilobium parviflorum*	0.73
managed crop pollinators	*Malva neglecta*	0.73
managed crop pollinators	*Centaurea scabiosa*	0.69
managed crop pollinators	*Hypericum perforatum*	0.55
managed crop pollinators	*Epilobium hirsutum*	0.55
managed crop pollinators	*Ranunculus acris*	0.46
managed crop pollinators	*Medicago lupulina*	0.41
managed crop pollinators	*Echium vulgare*	0.28
managed crop pollinators	*Galium mollugo*	0.23
managed crop pollinators	*Salvia pratensis*	0.23
managed crop pollinators	*Lolium multifloratum*	0.14
managed crop pollinators	*Silene pratensis*	0.14
managed crop pollinators	*Geum urbanum*	0.09
managed crop pollinators	*Leontodon hispidus*	0.09
managed crop pollinators	*Onobrychis viciifolia*	0.09
managed crop pollinators	*Salvia nubicola*	0.09
managed crop pollinators	*Anemone nemorosa*	0.09
managed crop pollinators	*Convolvulus arvensis*	0.09
managed crop pollinators	*Campanula rapunculoides*	0.09
managed crop pollinators	*Brassica napus*	0.09
managed crop pollinators	*Cardamine pratensis*	0.05

managed crop pollinators	*Galium album*	0.05
managed crop pollinators	*Ranunculus friesianus*	0.05
managed crop pollinators	*Solidago canadensis*	0.05
managed crop pollinators	*Urtica dioica*	0.05
managed crop pollinators	*Clematis vitalba*	0.05
managed crop pollinators	*Heracleum sphondylium*	0.05
managed crop pollinators	*Rumex acetosa*	0.05
managed crop pollinators	*Vicia cracca*	0.05
managed crop pollinators	*Geranium robertianum*	0.05
managed crop pollinators	*Phleum pratense*	0.05
managed crop pollinators	*Linaria vulgaris*	0.05
managed crop pollinators	*Reseda lutea*	0.05
rare bees	*Trifolium pratense*	12.16
rare bees	*Taraxacum officinale*	8.11
rare bees	*Vicia sepium*	6.76
rare bees	*Achillea millefolium*	5.41
rare bees	*Centaurea jacea*	5.41
rare bees	*Crepis capillaris*	5.41
rare bees	*Lotus corniculatus*	5.41
rare bees	*Knautia arvensis*	4.05
rare bees	*Potentilla neumanniana*	4.05
rare bees	*Origanum vulgare*	4.05
rare bees	*Ajuga reptans*	2.7
rare bees	*Picris hieracioides*	2.7
rare bees	*Silene flos cuculi*	2.7
rare bees	*Hypericum perforatum*	2.7
rare bees	*Echium vulgare*	2.7
rare bees	*Capsella bursa pastoris*	1.35
rare bees	*Geranium dissectum*	1.35
rare bees	*Glechoma hederacea*	1.35
rare bees	*Leontodon hispidus*	1.35
rare bees	*Leucanthemum vulgare*	1.35
rare bees	*Medicago lupulina*	1.35
rare bees	*Onobrychis viciifolia*	1.35
rare bees	*Plantago lanceolata*	1.35
rare bees	*Prunella vulgaris*	1.35
rare bees	*Rhinanthus alectorolophus*	1.35
rare bees	*Trifolium repens*	1.35
rare bees	*Veronica persica*	1.35
rare bees	*Campanula rapunculoides*	1.35
rare bees	*Erigeron annuus*	1.35
rare bees	*Potentilla sterilis*	1.35
rare bees	*Epilobium hirsutum*	1.35
rare bees	*Malva neglecta*	1.35
rare bees	*Tanacetum vulgare*	1.35
rare bees	*Hypericum hirsutum*	1.35
wild crop pollinators	*Trifolium pratense*	10.9
wild crop pollinators	*Lotus corniculatus*	8.61

wild crop pollinators	*Centaurea jacea*	8.21
wild crop pollinators	*Taraxacum officinale*	6.86
wild crop pollinators	*Rhinanthus alectorolophus*	5.52
wild crop pollinators	*Origanum vulgare*	5.38
wild crop pollinators	*Hypericum perforatum*	5.25
wild crop pollinators	*Vicia sepium*	4.71
wild crop pollinators	*Echium vulgare*	3.36
wild crop pollinators	*Malva neglecta*	2.96
wild crop pollinators	*Medicago sativa*	2.56
wild crop pollinators	*Achillea millefolium*	2.42
wild crop pollinators	*Knautia arvensis*	2.42
wild crop pollinators	*Ranunculus acris*	2.42
wild crop pollinators	*Trifolium repens*	2.42
wild crop pollinators	*Plantago lanceolata*	2.15
wild crop pollinators	*Ajuga reptans*	1.88
wild crop pollinators	*Leucanthemum vulgare*	1.75
wild crop pollinators	*Lamium galeobdolon*	1.35
wild crop pollinators	*Cirsium arvense*	1.35
wild crop pollinators	*Salvia pratensis*	1.21
wild crop pollinators	*Rhinanthus glaber*	1.21
wild crop pollinators	*Tanacetum vulgare*	1.21
wild crop pollinators	*Prunella vulgaris*	1.08
wild crop pollinators	*Crepis capillaris*	0.94
wild crop pollinators	*Silene flos cuculi*	0.94
wild crop pollinators	*Glechoma hederacea*	0.67
wild crop pollinators	*Veronica chamaedrys*	0.67
wild crop pollinators	*Dipsacus fullonum*	0.67
wild crop pollinators	*Ranunculus friesianus*	0.54
wild crop pollinators	*Daucus carota*	0.54
wild crop pollinators	*Euonymus europaeus*	0.54
wild crop pollinators	*Malva moschata*	0.54
wild crop pollinators	*Cota tinctoria*	0.4
wild crop pollinators	*Epilobium hirsutum*	0.4
wild crop pollinators	*Melilotus officinalis*	0.4
wild crop pollinators	*Lamium purpureum*	0.4
wild crop pollinators	*Geranium dissectum*	0.27
wild crop pollinators	*Veronica persica*	0.27
wild crop pollinators	*Anthriscus sylvestris*	0.27
wild crop pollinators	*Vicia cracca*	0.27
wild crop pollinators	*Erigeron annuus*	0.27
wild crop pollinators	*Galeopsis tetrahit*	0.27
wild crop pollinators	*Potentilla sterilis*	0.27
wild crop pollinators	*Silene pratensis*	0.27
wild crop pollinators	*Epilobium parviflorum*	0.27
wild crop pollinators	*Brassica napus*	0.27
wild crop pollinators	*Centaurea scabiosa*	0.13
wild crop pollinators	*Circaea lutetiana*	0.13
wild crop pollinators	*Medicago lupulina*	0.13

wild crop pollinators	*Onobrychis viciifolia*	0.13
wild crop pollinators	*Oxalis acetosella*	0.13
wild crop pollinators	*Picris hieracioides*	0.13
wild crop pollinators	*Cerastium fontanum*	0.13
wild crop pollinators	*Heracleum sphondylium*	0.13
wild crop pollinators	*Lamium maculatum*	0.13
wild crop pollinators	*Campanula rapunculoides*	0.13
wild crop pollinators	*Melilotus albus*	0.13
wild crop pollinators	*Rumex obtusifolius*	0.13
wild crop pollinators	*Stellaria media*	0.13
wild crop pollinators	*Cichorium intybus*	0.13
wild crop pollinators	*Lathyrus pratensis*	0.13
wild crop pollinators	*Linaria vulgaris*	0.13
wild crop pollinators	*Papaver rhoeas*	0.13

Table S4 Correlation table for all parameters with p-values above the matrix diagonal, and Pearson correlation values below the diagonal.

	total flower abundance	functional complementarity	total plant species richness	number of key plant species present	flower abundance of key species
total flower abundance		0.652	0.908	0.654	0.896
functional complementarity	-0.190		0.198	0.771	0.508
total plant species richness	-0.049	0.509		0.150	0.016
number of key plant species present	-0.189	0.123	0.559		0.086
flower abundance of key species	0.056	0.276	0.807	0.642	

CHAPTER 2

Local creation of wildflower strips and hedgerows in addition to high shares of landscape-scale greening measures promote multiple ecosystem services sustaining crop yield

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Manuscript formatted for and submitted to *Journal of Applied Ecology, in review*


Photo M. Tschumi

Local creation of wildflower strips and hedgerows in addition to high shares of landscape-scale greening measures promote multiple ecosystem services sustaining crop yield

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Abstract

1. The explicit and implicit aims of creating ecological focus areas (EFAs) and implementing greening measures in European agro-ecosystems include the promotion of regulatory ecosystem services (ES) to sustain crop production in conventional cropping systems. However, it remains poorly explored to what extent these goals are achieved with current policy measures.
2. We measured insect-mediated pollination and natural pest control service provisioning in 18 winter oilseed rape fields as a function of the independent and interactive effects of local EFA establishment ─ sown wildflower strips and hedgerows ─ and landscape-scale greening measures within a 1 km radius around focal fields and quantified their contribution to crop yield.
3. Insect pollination and pest predation increased by 10 and 13%, respectively, when landscape-scale greening measures were enhanced by 20%. For pollination, the increase was stronger in fields adjoining an EFA than in fields without adjacent EFA.

4. Agricultural management practices were the main drivers of crop yield. Pest predation, but not pollination, enhanced yield at average management intensity by 0.4 t/ha (9%) when predation increased by 50%. However, adjacent EFAs and landscape-scale greening measures did not influence crop yield directly.
5. ***Synthesis and applications.*** We conclude that the local establishment of perennial, plant species–rich wildflower strips and hedgerows combined with landscape-scale greening measures in agricultural landscapes can promote multiple ES in conventional production systems. These benefits may be maximized when local and landscape measures are combined. Direct effects of greening measures on final crop yield, however, seem to be less important compared to local agricultural management practices. Nevertheless, our findings should encourage also conventionally producing farmers to implement and maintain these EFAs. Further research is needed to better understand how the effectiveness of EFAs and other greening measures in promoting regulatory ES can be improved to minimize trade-offs, while promoting synergies, between ES provision, food production and biodiversity conservation.

Keywords: agri-environment schemes, biocontrol, canola, ecological intensification, functional biodiversity, landscape complexity, Meligethes, multiple ecosystem functioning, biocontrol, pollination, yield gain

Introduction

Among the multiple provisioning and supporting ecosystem services (ES) that contribute to crop production in agro-ecosystems, animal-mediated pollination (hereafter pollination) and natural pest control represent key services of paramount economic importance (Oerke 2005; Gallai *et al.* 2009). Pollination increases and stabilizes the yield of more than three quarters of the world's most important food crops (Klein *et al.* 2007; Aizen *et al.* 2009). Pest control is estimated to occur mainly through natural enemies (~50%) and host-plant resistance (~40%) and much less through pesticides (~10%) (Pimentel & Burgess 2014). The concept of agro-ecosystems in which multiple ES are optimized while anthropogenic inputs are minimized could represent a substantial step towards a more sustainable agriculture (Bommarco, Kleijn & Potts 2013). However, intensification of agriculture has occurred at the field scale, e.g. by increased inputs of agrochemicals, and at the landscape scale, e.g. by the reduction, simplification and fragmentation of habitats (Tscharntke *et al.* 2005). The concomitant loss of biodiversity has impaired the functioning of agro-ecosystems and the provisioning of multiple ES (Evenson & Gollin 2003; Pywell *et al.* 2012).

To mitigate the loss of biodiversity and important functions in agro-ecosystems, various measures have been realized (e.g. Ekroos *et al.* 2014). In the European Union (EU), agri-environment schemes have been implemented to support the development of rural areas and to protect biodiversity and ecosystem functions (European Union 2013). Since 2015, the EU common agricultural policy (CAP) has introduced greening measures as preconditions for farmers to obtain direct payments as part of the cross compliance system. Greening measures include crop diversification, the protection of permanent grassland from conversion to arable land and the implementation of ecological focus areas (EFAs) that encompass a series of specifically defined types of green infrastructure and semi-natural habitats (European Union 2014). In Switzerland, greening measures with a cross compliance mechanism have been in place since 1992, requiring the preservation or creation of EFA on 7% of the utilized

agricultural area (Bundesrat 2015). Whereas effects of greening and other agri-environmental measures on biodiversity have been studied repeatedly in Europe, including Switzerland (Kleijn *et al.* 2006; Aviron *et al.* 2009; Batáry *et al.* 2011), much less is known about the effectiveness of such measures in promoting multiple ES (but se e.g. Tschumi *et al.* 2016b for pest control as a single ES). Therefore, Swiss agricultural landscapes may serve as a laboratory for testing the possible consequences of the recent CAP reforms to estimate the effect of greening measures on the provisioning of multiple ES and their relevance for crop yield.

Responses of mobile ES providers, such as pollinators or pest antagonists, to local greening and other mitigation measures are likely contingent on the composition of the landscape and the amount, quality and configuration of such measures at the landscape scale (Scheper *et al.* 2013; Jonsson *et al.* 2015). The effects of a specific measure may therefore depend on the landscape context (Holzschuh *et al.* 2007). Two of the currently implemented EFA types, sown wildflower strips and hedgerows, whose effects were tested in this study, may have the potential to support multiple ES services through their structural and floral enhancement of the landscape (Wratten *et al.* 2012). For example, sown perennial, plant species–rich wildflower strips have recently been found to support natural pest control and provide resources for various potential ES providers (van Rijn & Wäckers 2015; Grass *et al.* 2016). Transient EFAs such as sown wildflower strips in arable areas rely on the colonization by ES providers from undisturbed long-lasting habitats. Therefore, the effectiveness of EFAs in delivering ES to a particular field is expected to depend on the share of additional greening measures in the surrounding landscape (Batáry *et al.* 2011; Scheper *et al.* 2013). However, we know very little about potential interactive effects of local EFAs and landscape-wide greening measures across spatial scales on the provisioning of multiple ES, and how such effects differ among EFA types and regulatory ES provided by various groups of mobile ES providers.

The ultimate goal of promoting regulatory ES is to sustain high crop yield (hereafter yield). However, yield is the result of a complex interplay of many influencing factors at various spatial and temporal scales. Crucial factors are the local climatic and soil conditions (Bartomeus, Gagic & Bommarco 2015) and crop management including crop rotation regime, nutrient input and pesticide applications. Recent studies suggest that regulatory ES provided by mobile organisms can interact in complex ways with local conditions and management in modulating crop yield (Bartomeus *et al.* 2014; Schneider *et al.* 2015; Marini *et al.* 2015; Bartomeus, Gagic & Bommarco 2015; Tschumi *et al.* 2016a). Moreover, multiple regulatory ES may interact synergistically in enhancing crop yield (Sutter & Albrecht 2016). The benefits of ES for crop yield are likely stronger in long-term converted organic production systems than in conventional systems (Birkhofer *et al.* 2015), as the effects of ES, in particular those of natural pest control services, may be masked anthropogenic inputs and more frequent tillage (Tilman *et al.* 2001). Whether and to what extent EFAs and other greening measures can increase multiple regulatory ES and final crop yield in conventional production systems, the current form of agriculture on over 90% of the European arable land (DG Agriculture and Rural Development 2013), remains largely unknown.

Here, we address these questions focusing on natural control of pests and pollination in winter oilseed rape *Brassica napus* L. (hereafter OSR), which is amongst the most important food, fodder and biofuel crops worldwide. Many pest species impose usage of phytosanitary products in OSR that could potentially be replaced by natural pest control to mitigate yield loss (Alford 2003). Furthermore, although OSR is considered to be mainly wind pollinated, recent studies have shown that the contribution of animal-mediated pollination to yield can be considerable (Bommarco, Marini & Vaissière 2012; Hudewenz *et al.* 2013; Bartomeus, Gagic & Bommarco 2015). Thus, there is high potential for ecosystem management measures to promote pollination and natural pest control services in conventional OSR production. To investigate the effect of adjacent EFAs and landscape-scale greening measures on pollination

and natural pest control in OSR and their influence on crop yield, we tested the four following interrelated hypotheses:

1. The local establishment of two commonly implemented types of EFAs (sown wildflower strips and hedgerows) enhances pollination and natural pest control service delivery in adjacent OSR crops.
2. The effectiveness of these adjacent EFAs in promoting pollination and natural pest control is reinforced by increasing the share of greening measures implemented at the landscape scale.
3. Insect pollination and natural pest control can increase final crop yield beyond agricultural management practices in conventional OSR production.
4. As consequence of 1–3, final OSR yield is enhanced in the presence of adjacent EFAs and increases with the share of greening measures at the landscape scale.

Materials and Methods

Study area and design

The study was conducted in 2014 in agricultural landscapes of the northern part of the central Swiss plateau (cantons Zurich and Aargau) characterized by a small-scaled mosaic of arable crops, grasslands and forest fragments. Eighteen OSR fields (hereafter focal fields) were selected adjacent to either a sown perennial, plant species–rich wildflower EFA strip (six fields) or an EFA hedgerow (six fields), or a conventionally managed crop (six fields; wheat, maize or rotational ley). For the detailed descriptions of seed mixture and management prescriptions of wildflower strips see Tschumi *et al.* (2016a). Hedgerows are linear woody elements containing at least five native shrub and tree species in any 10 meters and have a grassy margin (at least 3 m wide, 1–2 cuts a year, no fertilization). The two EFA types are part of the Swiss cross compliance system, and farmers receive direct payments for their implementation and maintenance. Focal fields next to each of the three adjacent habitat types ('wildflower strip', 'hedgerow' or 'no EFA') were selected along a gradient of landscape-scale greening measures in sectors of 1 km radius around the focal fields. The greening measure 'crop diversification' implemented in the CAP reform was not included in the hypotheses and analyses because it does not explicitly involve creation or management of habitats to specifically support mobile service providers and regulatory ES (European Union 2013). The selected landscape-scale greening measures encompassed permanent and extensively managed grasslands without fertilizer and pesticide inputs and EFAs including enhanced field margins, wildflower strips, hedgerows, forest edges (12 m buffer) and cover crop and leguminous crops (see Table S1 in Supporting Information). Although cover crop and leguminous crops make up only a relatively small proportion in the study region and are not part of the Swiss cross compliance (Table S1), these two land cover types were included in the analysis because they are listed as an EFA type promoted through the EU CAP greening. Within the six fields of each type of adjacent habitat the same gradient of landscape scale greening measures was covered, ensuring an unconfounded analysis of their single and interactive effects. All major

land cover types of each landscape sector were mapped in the field in the study year with a minimal mapping unit of 75 m^2 and entered in a Geographical Information System (ESRI, ArcMap 10.1) to perform calculations of proportions for all investigated habitat types (Table S1). To be able to buffer in-field heterogeneity occurring through differences in soil quality and other local factors, focal field measurements occurred at four distances (2, 9, 17 and 25 m) from the studied adjacent habitat type (18 focal fields × 4 in-field distances = 72 measurement points). The maximal in-field distance of 25 m was chosen based on the smallest studied field, such that each measurement point in the focal OSR field was always closer to the studied adjacent habitat than to any other bordering habitat of the focal field (see Fig. S1 for graphical representation of the in-field sampling design).

Measuring insect pollination

Twenty-four inflorescences of 12 OSR plants at each measurement point and focal field received two pollination treatments: open pollination (pollination of flowers occurred through autonomous, wind and insect pollination; 10 plants) and pollinator exclusion (two inflorescences of each plant were enclosed in nylon tulle bags with 1 × 1 mm mesh size; 2 plants). Bags of this mesh size do not hinder airborne pollen flow (Wragg & Johnson 2011) and are considered to be adequate to exclude insect pollinators for studying insect pollination in OSR (Bommarco, Marini & Vaissière 2012; Bartomeus *et al.* 2014; Garratt *et al.* 2014; Bartomeus, Gagic & Bommarco 2015). The beneficial effect of insect pollination on yield in OSR is mediated primarily by an increased number of developing seeds per fruit (hereafter seed set), although additional minor effects on seed quality (e.g. oil content) have been shown as well (Bommarco, Marini & Vaissière 2012; Sutter & Albrecht 2016). Thus, the difference in seed set between the two pollination treatments represents the main contribution of insects ('insect pollination') to crop yield. Bags were installed before the onset of flowering and removed immediately after flowers had withered. Shortly before commercial harvest, all fruits of each marked inflorescence were harvested and dried before seeds were counted and seed set

per fruit was calculated for each inflorescence. The chosen variety "V280OL" (Deutsche Saatveredelung AG 2016) was standardised for all but two fields to avoid confounding effects of differential response to pollination between cultivars.

Measuring predation and parasitism

The pollen beetle (*Meligethes aeneus* F.) is one of the major pests of OSR in Europe and causes damages of great economic importance. It is often controlled with applications of insecticides. Levels of natural pest control of pollen beetles were measured at all 72 measurement points with a method adapted from Büchi (2002), where larvae that naturally drop to the ground are either exposed to natural predation or experimentally protected from predation. This method allows to quantify two important pathways of natural control of the pollen beetle populations after fully grown larvae drop from the OSR flowers to the ground and before they pupate in the soil: (i) 'parasitism' (proportion of parasitized larvae, %) and (ii) 'predation' (predation rate of pollen beetle larvae on the ground by ground-dwelling arthropods in % = [number of pollen beetle adults emerging with exclusion of predators − number of adults emerging without exclusion of predators] / total number of larvae × 100). The two main natural enemy groups, flying hymenopteran parasitoids and predominantly ground-dwelling arthropods (Alford 2003), have very distinct life history traits and are likely influenced by drivers at different spatial scales. Therefore, parasitism and predation were assessed and analysed separately.

Sampling ES providers

At each measurement point and focal field, ground-dwelling arthropods were sampled with two pitfall traps. Jars (65 mm diameter) were filled with a 50% solution of ethylene glycol with a small volume of detergent. Traps were emptied weekly during the bloom of OSR, and catches were summed over the whole period for analysis. Ground beetles (Coleoptera: Carabidae), which are among the most important predators of pollen beetles

(Alford 2003), were identified to species level, and only the abundance of the predominant predatory species (according to Marggi 1992; Müller-Motzfeld 2004) included in the analysis.

Flower visitation by pollinators was surveyed twice in the morning and twice in the afternoon for 10 minutes each during OSR bloom in two 2 × 1 m plots at each measurement point of each focal field. Flower visitors were counted between 1000 and 1700 hours with good weather conditions (temperature above 13 °C with at least 60% clear sky and no wind). Wild bees and hoverflies are the most important wild pollinators of OSR in Europe (Jauker & Wolters 2008; Garratt *et al.* 2014). Numbers of flower visits by these two groups of wild pollinators, which directly rely on floral and nesting resources provided within the landscape, and those by managed honey bees (*Apis mellifera* L.) were analysed separately.

Field management data and yield measurements

Data on the management of focal OSR fields were collected through farmer interviews (mean values and ranges of all collected management variables are shown in Table S2). To determine agronomic yield (t/ha), a 2 m^2 plot was harvested at each measurement point of each focal field when fruiting was complete (seeds dry and fully developed), but before ripe fruits started to split and disperse seeds. The harvested material was dried and hand-threshed with a small stationary threshing machine (Wintersteiger Classic ST), and total seed mass was weighed and standardized to commercial humidity.

Statistical analysis

To test for the fixed effects of 'adjacent EFA' ('wildflower strip', 'hedgerow' or 'no EFA'), 'landscape-scale greening measures' and their interaction, the response variables 'insect pollination', 'predation' and 'parasitism' were modelled as two-vector response variables in generalized linear mixed-effect models with binomial error structure using the *R*-package *lme4* (Bates *et al.* 2014). To account for the multiple measurement points within each field, 'focal field' was included as random effect in the model. The numbers of ES providers

(‘wild pollinators’, ‘honey bees‘, ‘predatory ground beetles‘) pooled across sampling rounds were analysed using the same model structure, but fitted with a negative binomial error distribution, accounting for overdispersion present in the count data when using Poisson errors. Model selection based on likelihood-ratio tests followed recommendations by Zuur *et al.* (2009), and minimum adequate models were used for statistical inference.

To test for effects of ES on yield, while accounting for crop management, a two-step modelling approach was used. In the first step, the measured agronomic yield was fitted using a linear mixed effects model with ‘focal field’ as random effect. The full model included all collected independent and varying management variables and their two-way interactions (‘number of crops in rotation’, ‘number of insecticide applications’, ‘synthetic nitrogen fertilizer’, ‘plant density’, ‘seeding density’; see Table S2) as fixed explanatory variables. The number of insecticide applications serves as a good proxy for insecticide input levels in OSR as concentrations of active compounds in pesticide applications follow standard recommendations (Fachstelle Pflanzenschutz 2015). All other investigated or measured management parameters were excluded from the full model because they were either strongly correlated with one of the previously chosen parameters (field size, length of crop rotation, number of herbicide applications, number of fungicide applications; Pearson correlation coefficient > 0.7) or almost invariant between focal fields (seeding date, harvest date; see Table S2). After backwards model selection based on likelihood-ratio tests, all interactions and explanatory variables that could not explain a significant amount of variation were dropped, and the final model explaining yield contained only the two explanatory variables ‘number of insecticide applications’ and ‘OSR density’ and their interaction.

In the second step, the residuals of the above parameterised model were extracted and included as a response variable in a second linear mixed effects model with ‘predation’, ‘insect pollination’ and ‘parasitism’ as explanatory fixed effects and ‘focal field’ as random effect. The final model was selected based on likelihood-ratio tests, removing non-significant

variables. The predictions of this model are interpreted as the effect of ES on yield at average management intensity (Table S2). To additionally determine possible direct effects of 'adjacent EFA' and 'landscape-scale greening measures' and their interaction on yield, an linear mixed effects model was performed using the same structure and backward selection procedure as described for the previous analysis. For all models, assumptions were checked according to the graphical validation procedures recommended by Zuur *et al.* (2009). All statistical analyses were performed in R 3.2.3 (R Core Team 2015).

Results

Adjacent EFAs and landscape-scale greening measures driving ES providers and ES

The number of OSR flower visits by wild pollinators in focal fields tended to increase with 'landscape-scale greening measures' (Fig. 1a; Table 1). This increase was, however, dependent on the local presence of an EFA adjacent to the focal field, with higher flower visitation by wild pollinators in the presence of a wildflower strip or a hedgerow as compared with no adjacent EFA, as shown by the nearly significant effect of the interaction between both explanatory variables (Fig. 1a; Table 1). Honey bees, on the other hand, did not show any significant response to the tested explanatory variables (Table 1). Furthermore, both the presence of an adjacent EFA and landscape-scale greening measures increased the effect of insect pollination on seed set in focal fields (Fig. 1b; Table 1). Seed set driven by insect pollination was on average 10% higher when the focal field was adjacent to a flower strip and 4% higher when it was adjacent to a hedgerow compared with no adjacent EFA; furthermore, it increased from 7% at low (6%) to 18% at high (26%) proportions of greening measures in the landscape (Fig. 1b). However, there were no significant interactive effects of adjacent EFAs and landscape-scale greening measures on insect pollination (Fig. 1b; Table 1).

Predatory ground beetle abundance increased from 61 to 100 individuals along the gradient in landscape-scale greening measures but did not significantly differ among adjacent EFA types or control habitats (Fig. 1c; Table 1). However, pollen beetle predation increased significantly with landscape-scale greening measures from 10% at 6% to 23% at 26% landscape-scale greening measures (Fig. 1d; Table 1), but no significant effect of the adjacent EFA could be detected either. Parasitism of pollen beetle larvae (8% on average) was independent from adjacent EFA and did not change with increasing landscape-scale greening measures (Fig. 1d; Table 1).

Effects of ES on OSR yield

Pollen beetle predation significantly contributed to crop yield after accounting for crop management with a predicted increase in OSR yield by 0.4 t/ha (9%) when predation increased from 0 to 50% (Fig. 2; Table 1). Insect pollination and parasitism did not significantly contribute to OSR yield after accounting for management intensity, and there were no significant interactive effects among the measured ES on OSR yield (Fig. 2; Table 1). Furthermore, neither adjacent EFA nor landscape-scale greening measures or their interaction had significant direct effects on OSR yield (Table 1).

Discussion

Effects on pollinators and insect pollination

Higher proportions of landscape-scale greening measures and the local presence of perennial wildflower strips and hedgerows adjacent to the focal field synergistically increased OSR flower visitation by wild pollinators. Their interactive effect suggests that adjacent EFAs on their own do not provide enough food, overwintering and nesting resources for wild pollinators such as wild bees and hoverflies to optimally sustain local populations. Increased OSR flower visitation occurred only in landscapes with a relatively large share of greening measures that likely act as reservoirs and ensure large species pools. Furthermore, in landscapes with a high share of greening measures, OSR crops adjacent to sown wildflower strips received higher flower visitation rates and pollination services than those bordered by hedgerows. This higher effectiveness of wildflower strips compared to hedgerows in promoting pollination services is probably due to the continuously available, abundant and diverse floral resources provided by the flowering species–rich perennial wildflower strips. Wildflower strips also included a considerable proportion of unshaded open soil, which likely matches the nesting requirements of the mainly soil-nesting wild bees visiting OSR flowers in our study (Potts *et al.* 2005; Zurbuchen & Müller 2012). In addition, a remarkably high density of vole burrows were observed in the investigated perennial flower strips (M. Albrecht, personal observation), which are often used as nest building sites by bumblebee species such as *Bombus terrestris* L. and *Bombus lapidarius* L. (Kells & Goulson 2003), two of the most important wild pollinator species of OSR in the study region (L. Sutter, unpublished). In contrast, hedgerows flower very early but provide less continuous food resources during the year. Although hedgerows may be important for cavity-nesting bees relying on dead wood or hollow stems as nesting resources, these bees are typically less abundant and thus functionally less important for OSR pollination in Europe (e.g. Garratt *et al.* 2014; L. Sutter, unpublished).

As expected, honey bees were not significantly affected by greening measures, probably because they do not depend on nesting opportunities. Their density in the landscape rather depends on the number of honey bee hives. Highly attractive and abundantly flowering EFAs and other habitats synchronously flowering with OSR may even keep honey bees and other pollinators away from OSR crops. However, in the present study, such a suggested competitive effect of highly attractive did not occur; flower visitation rates by honey bees across the focal OSR fields were not affected by any greening measure.

Effects on predatory ground beetles and natural pest control

The gradient in landscape-scale greening measures from 6 to 26% tended to increase the number of predatory ground beetles in the investigated OSR fields by 39% regardless of whether an EFA was adjacent or not. Although most predatory ground beetles rely on semi-natural habitats at least once during their life cycle (Pywell *et al.* 2005), direct vicinity of these habitats was not crucial here contrary to results of other studies (e.g. Duflot *et al.* 2016). In contrast, the herein found positive effect of landscape-scale greening measures on ground beetle abundance does not suggest that particular greening elements of the landscape may play a significant role whereas a general spatial heterogeneity of the wider landscape might be decisive (Bertrand, Burel & Baudry 2015). The strong increase in predator abundance at high proportions of greening measures implemented at the landscape scale was reflected in a considerably stronger pest suppression by 13% when landscape-scale greening measures increased by 20%.

Parasitism of OSR pollen beetles on the other hand did not significantly vary with the share of landscape-scale greening measures. Findings of previous studies investigating the effects of the landscape-scale proportion of semi-natural habitat on pollen beetle parasitism are ambiguous (Thies & Tscharntke 1999; Zaller *et al.* 2008; Visser *et al.* 2009; Rusch *et al.* 2011). In our study, parasitism rates were relatively low (8% on average), which may be explained by an extraordinarily cold spring in the study year with rather low or delayed

emergence of hymenopteran parasitoids combined with insecticide applications before OSR flowering (Ulber, Klukowsik & Williams 2010). The strong effects of greening measures on predators and predation leads to the conclusion that predation, and not parasitism, of the pollen beetle is the major driver of natural pest control in our study.

Effects of ES on yield

Increased pollination and natural pest control services do not necessarily translate into enhanced crop yield (Bos *et al.* 2007; Klein *et al.* 2014). A key finding of our study is that a 50% increase in predation by natural enemies on the main pest of European OSR production, the pollen beetle, indeed increased agronomic crop yield under conventional production by 9% at average management intensity. Higher yield with increasing predation could be a combination of pest-induced compensatory growth by plants and strong predation. It has been reported that moderate feeding damage to the terminal raceme of OSR plants leads to increased production of new side racemes (e.g. Pinet, Mathieu & Jullien 2015). If minor plant damage triggers a compensatory response to produce more biomass, this increase outweighs the feeding damage such that no reduction arises. If compensation co-occurs with strong natural pest control and optimal growth conditions, it may even lead to higher overall yields. Bartomeus, Gagic & Bommarco (2015) hypothesized that such a compensatory growth is beneficial only under strong pollination and may indicate that the benefits can arise only if these newly produced flowers are well pollinated. Pollination, however, did not play a significant role for final crop yield in the present study, presumably because seed set in the studied OSR variety is not as strongly limited by insect pollination as in other varieties in which the contribution of insect pollination ranges between 13 and 50% (Hudewenz *et al.* 2013; Marini *et al.* 2015; Sutter & Albrecht 2016). The relatively low pollinator dependence of the investigated variety is likely also the main reason for the lack of significant interactive effects among pollination and natural pest control services found in the present study, despite experimental evidence for strikingly strong interactive effects among pollination and pest

control shaping final yield of another OSR variety (Sutter & Albrecht 2016). Furthermore, the weaker contrasts in pollinator visitation rates and natural pest control levels along with the inherent higher complexity of the ecosystems studied here may have contributed to the lack of significant interactive effects.

Conclusions and Management Implications

Agriculture has to meet the growing demand for food while minimizing negative impacts on biodiversity and ecosystem functioning. It is hoped that the implementation of greening measures helps to achieve this goal by promoting farmland biodiversity and ES that sustain high and stable crop yields. Our results suggest, however, that beneficial effects of greening measures on the regulatory ES pest control and insect pollination in conventional OSR production become relevant only at increases in proportions of greening measures–much higher than the currently required 5% greening measures in the EU. However, the agricultural landscapes studied here did not comprise highly simplified and cleared landscapes largely lacking any greening elements or other semi-natural habitats. Regulatory ES may be restored and considerably enhanced already at lower increases in greening measures implemented in such landscapes. Furthermore, it is important to note that we investigated effects of greening measures in intensive, conventional OSR production systems. Through reduced negative effects of pesticides in organic crop production, the effect of multiple ES for crop yield are expected to be more robust compared to conventional production systems that still mainly rely on anthropogenic inputs. However, organic agriculture usually needs more land to produce the same quantity of food compared with conventional production. Whereas the conventional production system studied here represents the prevailing form of agriculture in Europe, highlighting the importance of evaluating the consequences of EFAs and greening measures for the provisions of regulatory ecosystem services in these systems. Although final crop yield was mainly driven by management practices rather than greening measures, our study shows that both the local creation of EFAs, such as species-rich, perennial wildflower strips and

hedgerows, nearby OSR crops and a considerable landscape-scale augmentation of greening measures can promote multiple regulatory ES to sustain crop yield even in conventional production systems. Our findings of beneficial effects of local and landscape-scale implementation of EFAs and other greening measures on important regulating ES may help to encourage farmers to implement them. Further research is needed to investigate how EFAs and other greening measures can be improved to make them more effective in achieving their multiple goals. Future studies should especially consider trade-offs and synergies at large scale between ES provision, food production and biodiversity conservation needs.

Acknowledgements

We thank Stephan Bosshart, Amélie Mandel, Marco Labarile, Neil Rafferty, Benno Zehnder, Marc Fässler, Gisela Lüscher, Nina Richner and Felix Herzog for their help with the fieldwork, Werner Marggi for the identification of ground beetles and Jonas Winizki, Erich Szerencsits and Dario Oertle for GIS-support. Protocols were developed jointly with the QuESSA project partners. The work could not have been carried out without the support of farmers who graciously let us work on their properties. We are grateful to Felix Herzog, Owen Petchey, Bernhard Schmid and Matthias Tschumi for valuable discussions and helpful comments on an earlier version of the manuscript.

Data accessibility

All data associated with this manuscript will be available at the Dryad Digital Repository upon acceptance of this manuscript.

Table

Table 1 Results of final generalized linear mixed-effects models after removing non-significant explanatory variables. Likelihood-ratio tests with shown denominator degrees of freedom (d.f.), and *P* values from χ^2-test. Significant *P* values ($P < 0.05$) are shown in bold (see Materials & Methods section for detailed description of explanatory variables, response variables and statistical models)

Response	Fixed effects	d.f.	χ^2	*P* value	
Wild pollinator visits	Adjacent EFA : Landscape-scale greening	2	5.265	0.072	.
	Adjacent EFA	2	1.574	0.455	NS
	Landscape-scale greening	1	2.138	0.144	NS
Honey bee visits	Adjacent EFA : Landscape-scale greening	2	1.473	0.479	NS
	Adjacent EFA	2	0.544	0.762	NS
	Landscape-scale greening	1	1.342	0.247	NS
Insect pollination	Adjacent EFA : Landscape-scale greening	2	1.422	0.491	NS
	Adjacent EFA	2	10.09	**0.006**	*
	Landscape-scale greening	1	6.196	**0.013**	*
Predatory ground beetles	Adjacent EFA : Landscape-scale greening	2	2.600	0.273	NS
	Adjacent EFA	2	1.227	0.541	NS
	Landscape-scale greening	1	4.329	**0.037**	*
Predation	Adjacent EFA : Landscape-scale greening	2	3.257	0.196	NS
	Adjacent EFA	2	0.453	0.797	NS
	Landscape-scale greening	1	6.040	**0.014**	*
Parasitism	Adjacent EFA : Landscape-scale greening	2	3.257	0.196	NS
	Adjacent EFA	2	2.199	0.333	NS
	Landscape-scale greening	1	0.290	0.590	NS
Yield	Predation : Pollination : Parasitism	1	0.215	0.643	NS
	Predation : Pollination	1	1.172	0.279	NS
	Predation : Parasitism	1	2.484	0.115	NS
	Pollination : Parasitism	1	0.023	0.878	NS
	Predation	1	6.093	**0.035**	*
	Pollination	1	0.208	0.648	NS
	Parasitism	1	1.963	0.161	NS
Yield	Adjacent EFA : Landscape-scale greening	2	0.435	0.804	NS
	Adjacent EFA	2	0.421	0.810	NS
	Landscape-scale greening	1	0.004	0.948	NS

Figure 1

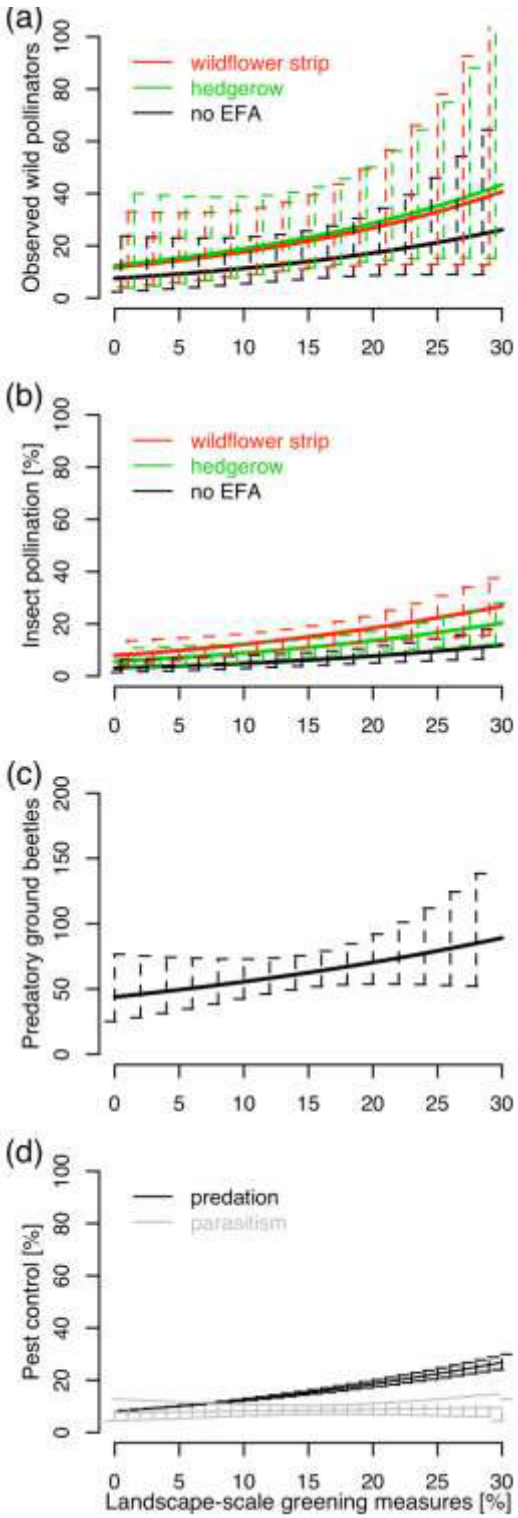


Figure 1 Effects of landscape-scale greening measures and adjacent EFA (wildflower strip (red), hedgerow (green), and no EFA (black)) on (a) number of observed wild pollinator, (b) increase of seed set driven by insect pollination (%), (c) number of predatory ground beetles, (d) predation on pollen beetle (black) and pollen beetle parasitism (grey). Predicted values

±95% confidence interval for the investigated gradient (6–26%) of landscape-scale greening measures (n = 18 fields). Where no differences between adjacent habitat types occurred, only the average values for all three habitat types is shown.

Figure 2

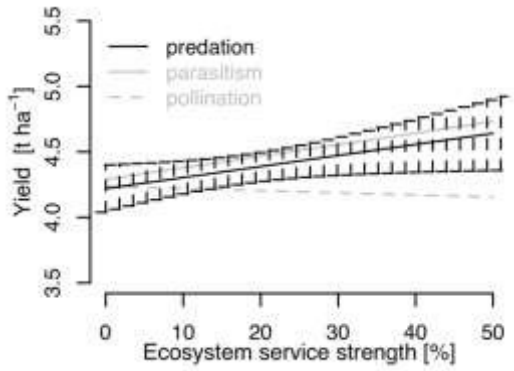


Figure 2 Effect of measured ES ('ES Strength') on yield after accounting for management: predation (black line), parasitism (grey solid line) and insect pollination (grey dashed line). Predicted values for observed range in ES strength ±95% confidence interval (only for significant parameters).

Supporting Information

Table S1 Summary statistics of land cover categories.

Table S2 Summary statistics describing indicators of field management.

Figure S1 Layout of in-field measurement points.

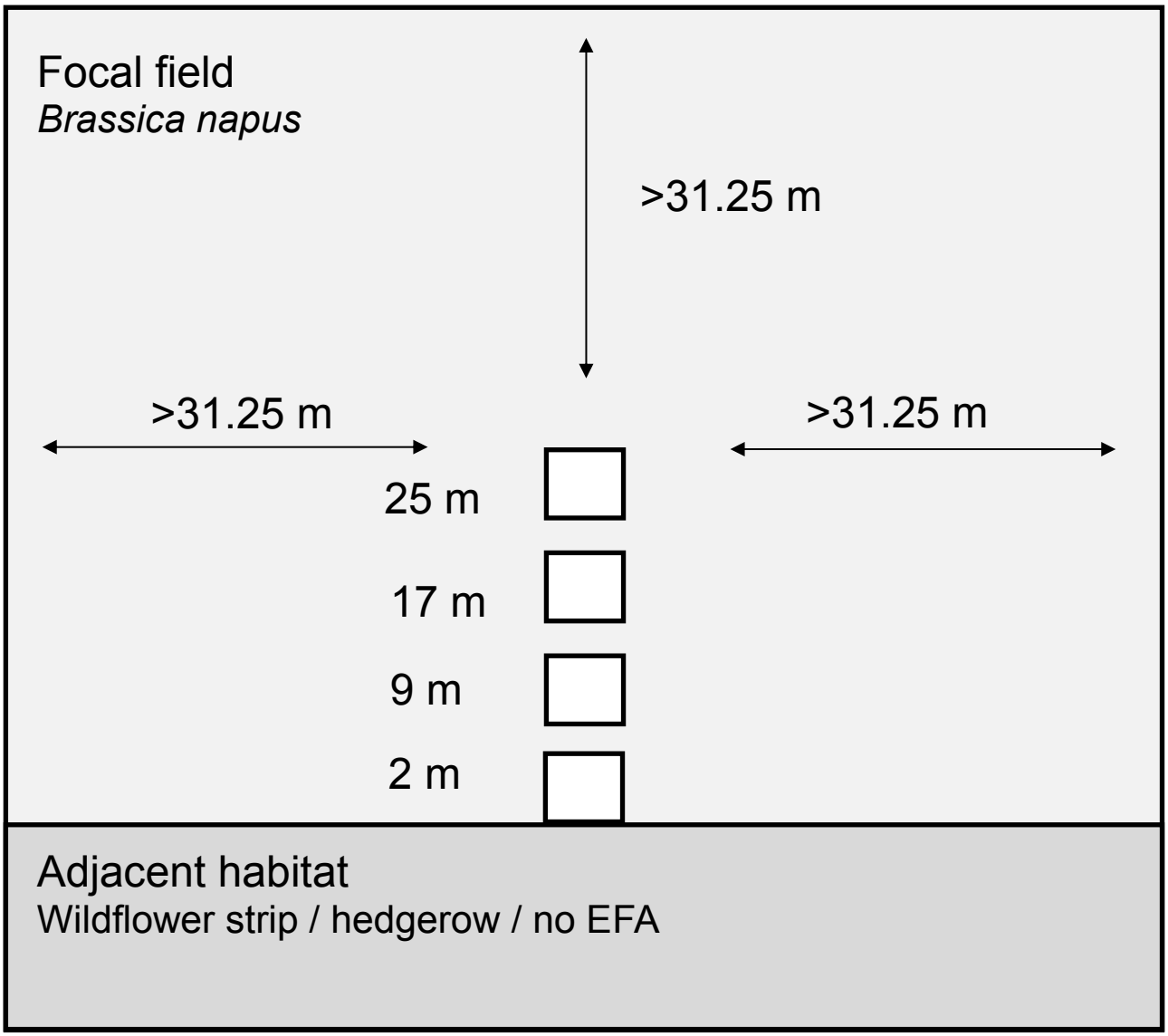
Table S1 Descriptive statistics of land cover (in %) within landscape sectors of 1 km radius around focal fields. Arable crops covering less than 1% are not listed here. Shown are arithmetic means (mean), minima (min.) and maxima (max.).

Class	Land cover type	mean	min.	max.
Arable crop	Wheat (*Triticum aestivum*)	10.6	5.0	17.3
Arable crop	Rotational ley	8.8	2.0	17.9
Arable crop	Maize (*Zea mays*)	8.3	2.0	16.1
Arable crop	Forage crop	4.3	0.0	10.4
Arable crop	Sugar beet (*Beta oleracea*)	3.3	0.0	7.6
Arable crop	Oilseed rape (*Brassica napus*)	3.3	0.9	6.8
Arable crop	Barley (*Hordeum sativum*)	2.4	0.2	4.6
Arable crop	Commercial horticulture	1.3	0.0	7.5
Arable crop	Potato (*Solanum tuberosum*)	1.2	0.0	6.3
Arable crop	Rye (*Secale cereale*)	1.1	0.0	3.4
Greening	Strips along forest edges	7.3	4.4	18.9
Greening	Permanent extensive grassland	4.7	0.4	14.1
Greening	Hedges or wooded strips	1.7	0.2	4.6
Greening	Margins, ditches, flower and buffer strips, fallow land	1.1	0.2	3.1
Greening	Peas (*Pisum* spp.)	0.3	0.0	2.3
Greening	Alfalfa (*Medicago sativa*)	0.2	0.0	0.8
Greening	Field beans (*Vicia faba*)	0.1	0.0	0.5
Greening	Soja (*Glycine max*)	0.1	0.0	1.2
Greening	Catch crops and green cover	0.1	0.0	0.9
Matrix	Forest	20.4	3.8	45.5
Matrix	Urban area	10.5	0.1	42.9
Matrix	Roads	0.9	0.0	6.0
Matrix	Water bodies	0.7	0.0	4.6

Table S2 Summary statistics describing indicators of field management on 18 investigated OSR fields that were included in the yield model (MOD) or excluded because of strong correlation (COR) or invariance (INV).

	Field measures	***n***	**Mean ± s.e.m**	**Median (range)**
MOD	No. of crops in rotation	18	3.83 ± 0.15	4 (3–5)
MOD	No. of insecticide applications	18	2.33 ± 0.30	3 (0–4)
MOD	Synthetic nitrogen fertilizer (kg N ha^{-1})	18	96.33 ± 15.64	102.50 (0.00–192.50)
MOD	Plants density (No. of plants m^{-2})	18	54.69 ± 3.74	57 (32–90)
MOD	Seeding density (g m^{-2})	18	46.36 ± 3.16	50 (25–65)
COR	Field size (ha)	18	1.94 ± 0.28	1.45 (0.82–5.36)
COR	Length of crop rotation (years)	18	4.44 ± 0.17	4 (4–6)
COR	No. of herbicide applications	18	0.94 ± 0.19	1 (0–3)
COR	No. of fungicide applications	18	0.89 ± 0.18	1 (0–2)
INV	Seeding date	18	01.09.13 ± 0.98	03.09.13 (22.08.13–08.09.13)
INV	Harvest date	18	20.07.14 ± 1.17	18.07.14 (16.07.14–02.08.14)
	Yield (t ha^{-1})	18	4.37 ± 0.33	4.10 (1.98–6.90)

Figure S1 Layout of in-field measurement points.



CHAPTER 3

Synergistic interactions of ecosystem services: florivorous pest control boosts crop yield increase through insect pollination

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Manuscript formatted for and published in *Proceedings of the Royal Society B:* **283** 20152529

Synergistic interactions of ecosystem services: florivorous pest control boosts crop yield increase through insect pollination

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Abstract

Insect pollination and pest control are pivotal functions sustaining global food production. However, they have mostly been studied in isolation and how they interactively shape crop yield remains largely unexplored. Using controlled field experiments we found strong synergistic effects of insect pollination and simulated pest control on yield quantity and quality. Their joint effect increased yield by 23%, with synergistic effects contributing 10%, while their single contributions were 7% and 6% respectively. The potential economic benefit for a farmer from the synergistic effects (12 %) was 1.8 times greater than their individual contributions (7 % each). We show that the principal underlying mechanism was a pronounced pest-induced reduction in flower lifetime, resulting in a strong reduction in the number of pollinator visits a flower receives during its lifetime. Our findings highlight the importance of non-additive interactions among ecosystem services when valuating, mapping or predicting them and reveal fundamental implications for ecosystem management and policy aimed at maximising ecosystem services for sustainable agriculture.

Keywords: multiple ecosystem services, flower withering, herbivory, pollen beetle

Introduction

Ecosystem services (hereafter ES) encompass a large set of goods and functions provided by ecosystems, vital for human well-being (Daily, Naylor & Ehrlich 1997). While the global demand for reliable provisioning of ES is increasing, many of these services are declining due to anthropogenic driven ecosystem changes (Vitousek 1997). Considerable effort has been made to quantify, map and identify the drivers and consequences of individual ES in agriculture (Bommarco, Kleijn & Potts 2013), and it is increasingly recognized that ES rarely act in isolation, but interact with each other in complex ways (Bennett *et al.* 2009; Classen *et al.* 2014). Alterations in shared drivers can indirectly result in synergies or trade-offs between multiple ES and a range of potentially profound positive or negative interactive effects (Bennett *et al.* 2009). Consequently there have been repeated calls for research aimed towards a better understanding of the relationships among multiple ES, and their underlying mechanisms, as a prerequisite for effective ecosystem management to sustainably maximise ES (Bennett *et al.* 2009; Seppelt *et al.* 2011). Maximising multiple ES in agro-ecosystems is crucial to meet the challenge of long-term food security through sustainable crop production, without jeopardizing biodiversity and ecosystem health (Kennedy *et al.* 2013). To achieve this goal, we need to understand if and how the management of one service has positive, negative, or negligible effects on other services.

Among the multiple provisioning and supporting ES which contribute to yield in agro-ecosystems, animal-mediated crop pollination (hereafter pollination) represents a key service with an estimated economic value for global crop production of € 153 billion per year (Gallai *et al.* 2009). At the same time approximately one third of the potential global crop yield is lost to pests (Oerke 2005), highlighting the enormous potential and urgent need for pest control. Pollination directly increases and stabilizes the yield of ca. 70% of the world's most important crops (Klein *et al.* 2007; Aizen *et al.* 2009). Pest control directly reduces the negative impact of pests on crop plants (Daily, Naylor & Ehrlich 1997). While the importance of pollination

and pest control for crop production are well recognized individually (Losey & Vaughan 2006; Klein *et al.* 2007), their interactive effects on crop yield and farmer's economic gain remain largely unexplored. The few studies that have recently started to explore the combined effects of pollinaton and pest control suggest that such interactions may indeed exist (Lundin *et al.* 2013; Bartomeus, Gagic & Bommarco 2015), but unfortunately we still lack (i) a robust quantification of the effect size of such interacive effects compared to their single effects, which would enable the contribution of such interactive effects on the final crop yield and its economic importance to be assessed; (ii) a mechanistic understanding of ecological drivers governing interactive effects among pollination and pest control. However, a quantitative knowledge of the economic importance of the potential interactive effects of pollination and pest control on crop yield, and a better understanding of the mechanisms driving such effects, is fundamental in order to reliably valuate and predict interactive effects, and those of their potentially shared drivers, such as land-use- or climate change (Schröter *et al.* 2005). This is a vital pre-requisite for improved management of agro-ecosystems and ecological intensification (*sensu* Bommarco, Kleijn & Potts 2013).

In this study we experimentally examine the single and combined effects of pollination and simulated pest control shaping yield quantity and quality in winter oilseed rape *Brassica napus* L. (hereafter OSR). OSR is amongst the most important food, fodder and biofuel crops worldwide, and its economic importance has continuously increased in the last years. Yield losses of OSR due to herbivory by the pollen beetle *Meligethes aeneus* Fab. can be severe without pest control (Alford 2003). Although OSR is considered to mainly be pollinated through wind, recent studies indicate that the contribution of animal-mediated pollination to OSR yield can be considerable (Bommarco, Marini & Vaissière 2012; Hudewenz *et al.* 2013). Thus interactive effects of pest control and animal pollination in OSR production may be of great economic importance, yet remain to be experimentally explored.

The potential non-additive effects of pollination and pest control, which shape crop yield, may occur via a multitude of pathways. Here, we test three hypothetical mechanisms (M1-M3). Such effects could arise where alterations in the attractiveness of crop plants to pollinators ─ through changes in floral traits or direct repellence of pollinators by florivorous pests ─ reduce flower visitation and thereby pollination services (Krupnick, Weis & Campbell 1999) (M1); through compensatory responses of crops to herbivory by pests, such as compensatory growth (Munguía-Rosas *et al.* 2015) or even over-compensation (Chiariello & Gulmon 1991) resulting in overall higher yields (M2). A further potentially important, but to our knowledge unexplored, synergistic effect of pollination and control of florivorous pests may act via florivorous pest-induced changes in flower lifetime (M3). In OSR for example, flower lifetime is shorter if pollen is removed from the stamens (Bell & Cresswell 1998). If florivorous pests remove pollen from the anthers, thereby reducing the lifetime of flowers, the probability of a flower being visited and the average number of visits a flower receives by pollinators during its lifetime may be reduced.

The main objectives of the present study are therefore (l) to quantify the relative importance of animal pollination and pest control, and in particular their interactive effects on OSR yield quantity and quality, and the potential economic value of these effects and (ll) to test the mechanistic pathways (M1-M3) driving potential interactive effects among pest control and pollination. We show that the potential economic benefit for a farmer from synergistic effects is 1.8 times greater than the individual contributions of pollination and pest control and provide a mechanistic explanation for this striking finding. Our findings reveal the importance of taking non-additive pollination-pest control interactions into account when predicting and managing multiple ecosystem services for sustainable food production.

Materials and methods

Study system

Oilseed rape (OSR) production in Europe suffers from a series of herbivorous pests. The most severe yield losses in Europe (up to 100% without pest control) are due to herbivory by the pollen beetle, *Meligethes aeneus* Fab. (Coleoptera: Nitidulidae) (Alford 2003). The adult beetles feed on the pollen of open and closed flowers, the latter leading to flower development abortion and consequently reduced fruit set. OSR is considered to mainly be pollinated by wind, because currently grown cultivars with restored fertility are self-fertile, but recent evidence suggests that insect pollination can significantly increase seed set in commonly grown varieties (Hudewenz *et al.* 2013). Bumblebees, in particular the buff-tailed bumblebee *Bombus terrestris* L. (Hymenoptera: Apidae, hereafter "bumblebees") together with honey bees and a series of solitary bee and hoverfly species are the most important pollinators of OSR in Europe (Garratt *et al.* 2014).

Experimental design

The experiment was conducted in spring 2014 at Agroscope-Reckenholz (lat 47.430868°, long 8.518491°, 442 m.a.s.l) in Zurich, Switzerland. An area of 0.9 ha was sown in early September 2013 with the winter OSR variety "Visby" (Rapool-Ring GMBH Isernhagen, Germany), a commonly grown OSR variety in Central Europe. The entire field was managed according to standard practices of conventional OSR production until the establishment of the experimental treatments. Immediately after the fertilizer application in early spring, 24 cages (4 × 2 × 2 m) were assembled − before colonisation of the field by pollen beetles. Cages were spaced 4 m apart from one another to avoid reciprocal shading. They were covered with a fine mesh fabric (HD-polyethylene, 0.74 × 1.12 mm; Howitec, The Netherlands) which excludes pollinators, pollen beetles and their natural enemies, including small Hymenopteran parasitoids and ground dwelling arthropods, but should not affect wind pollination of the caged plants (Wragg & Johnson 2011). Cages were randomly assigned to

one of four treatments (n = 6) in a fully crossed design with two pollination levels (pollination vs. no pollination) crossed with two pest control levels (weak vs. strong pest control). Cages were arranged within six spatial blocks on the experimental field such that each block contained one cage of each of the four treatments.

Simulated pest control treatment

Pest (pollen beetle) control was simulated by experimentally establishing two different pollen beetle densities in the cages, with 12 cages per simulated pest control treatment. This experimental pest control thus reflected pest control irrespective of the identity of the pest control agent, and ensured that the level of pest control could be precisely und uniformly established at field-realistic levels for the two treatments (Lundin *et al.* 2013). To simulate a strong level of pest control we added a total of ~1600 adult pollen beetles to each of 12 randomly selected cages, resulting in approximately nine beetles per caged OSR plant (~ 3 beetles per main raceme, see e.g. (Schneider *et al.* 2015)). This corresponds to a situation with successful pest control, reducing pest levels below the threshold where no significant yield loss is expected (Agridea. (2014) Bekämpfungsschwellen im Ackerbau, www.agridea.ch), even when assuming a negative linear relationship among pollen beetle density to OSR yield (Schneider *et al.* 2015). In each of the remaining 12 cages roughly four times more pollen beetles (~6800 adults, resulting in approximately 36 beetles per plant) were introduced. These densities, subsequently monitored to test for treatment performance, corresponded to average natural densities of adult pollen beetles in OSR fields in the study region during colonisation by pollen beetles (Sutter, unpublished). Adult pollen beetles were collected by sweep netting surrounding OSR fields and were introduced into the cages at the time of natural pollen beetle colonisation of OSR fields in the study region.

Insect pollination treatment

Shortly after the onset of flowering, on 14 April 2014, half of the randomly selected cages of both pest control treatments were each equipped with a colony of *Bombus terrestris*

consisting of a queen and approximately 9 - 12 workers ("mini hive", Biobest, Westerlo, Belgium). Bumblebee hives were mounted 15 cm above the ground and protected against rain with a plastic roof. To achieve natural levels of OSR flower visitation under field conditions, the number of bumblebee workers and the amount of time they were allowed to visit OSR flowers in cages was controlled by adjusting the time the hive's separate inlet and outlet hole was open based on the following formula:

$$\text{"Bumblebee hours"} = V_{rate\ flower\ field} \times L \times F_{tot\ cage} / V_{rate\ single\ worker\ field}$$

where $V_{rate\ flower\ field}$ is the observed flower visitation rate by pollinators in the study region under field conditions (Sutter, unpublished field study), L is the average flower lifetime [h] observed under field conditions (Bell & Cresswell 1998), $F_{tot\ cage}$ is the estimated total number of flowers per cage (estimated at the beginning of the experiment, this study) and $V_{single\ worker\ field}$ is the average number of OSR flower visits per time observed for a single *B. terrestris* worker under field conditions (Hayter & Cresswell 2006). The estimated value of "bumblebee hours" obtained by this formula tells us how many bumblebee workers are allowed to forage for how long in a cage to achieve visitation rates of caged OSR flowers that are in the range of natural visitation rates of OSR flowers under field conditions in the study region. During the remaining time period bumblebees fed on a sugar solution provided inside the hive.

Pollinator visits and flower phenology

Flowering onset, flower lifetime, and flower visitation by pollinators were assessed for both pest control treatments. At each of three observation rounds during the flowering period of OSR the number of flowers visited and the time spent on a single flower (visit duration) of each of two bumblebee workers was recorded during two minutes (200 visits recorded on average per cage). The time of day of observations was randomized across cages and observation rounds and pest control treatments. Flower abundance (i.e. Number of open flowers in a 50x50 cm wooden frame, averaged over 4 counts in different places, calculated

for the cage area) was estimated on each observation date, which was used to estimate average pollinator visitation rate per flower of each cage.

To detect potential differences in flowering onset, the total number of open flowers of 10 randomly selected plants of each cage was counted at the beginning of the flowering period, before pollinators were introduced into the cages. To test for possible differences in flower lifetime among treatments, all open (but not yet senescent; hereafter "open") flowers of the main shoot inflorescence of 10 randomly selected plants of each cage were counted and marked (using fine wire tagging the upper and lower limit of the range of open flowers). Because senescence (*sensu* Bell & Cresswell 1998) could not be observed directly, the number of senescent flowers and the number of flowers still open from the previous marking were counted 72 hours later. To calculate the relationship between the percentage of senescent flowers and flower lifetime, a calibration was necessary. To this end an additional experiment was conducted, in which 10 independent inflorescences of potted OSR plants with 10 freshly opened flowers each were exposed to different densities of adult pollen beetles (0, 0.1, 0.5, 1, 5 pollen beetles per OSR flower; n = 10 for each pollen beetle level). Flower lifetime and the proportion of senescent flowers were recorded. As flower lifetime (L) and the proportion of senescent flowers after 72h (P_{tot}) are linearly proportional ($L = 0.2824 \times P_{tot} + 9.72$; $R^2 = 0.97$), the slope of this relationship allows the calculation of flower lifetime from the percentages of senescent flowers measured in the cages. This experiment was also used to demonstrate and parameterise the negative relationship between pollen beetle density and flower lifetime. Reducing flower lifetime can consequently reduce the number of pollinator visits per flower lifetime (M3). These results are shown in Fig. S1. The number of pollinator visits a single flower receives during its lifetime (V_{tot}) was then estimated for each cage as:

$$V_{tot} = L \times V_{rate} / F_{tot}$$

Where L is the estimated average flower lifetime per cage [h], V_{rate} is the total number of flower visits per cage during one hour [visits × h^{-1}] and F_{tot} is the estimated total number of flowers per cage.

Yield measurements

Yield and other plant parameters were determined for 10 randomly selected OSR plants of each cage, collected on the 17 July 2014, when fruiting was complete (seeds dry and fully developed), but before ripe fruits started to split and disperse seeds. For each harvested plant the total number of shoots was measured. Additionally, the total number of fruits containing seeds (fruit set) of each main and fifth side shoot was measured. For each of these shoots, seed set (i.e. the mean number of seeds per fruit), mean seed mass (i.e. the mean weight of 1000 seeds) and total seed mass per fruit (i.e. mean seed mass × seed set) were measured for ten randomly selected fruits per shoot. Shortly after harvesting these ten plants, each entire (previously caged) 2 × 4 m plot was threshed with a threshing machine (Wintersteiger Classic Plot Combine). In addition to the standard quantitative measure of agronomic yield (seed mass of threshed plants per cage [t ha^{-1}]; hereafter "yield"), we analysed the oil content of the pooled seeds of the threshed plants per cage [g kg^{-1}] with Near Infrared Spectroscopy NIRS (Foss NIRSystem, Inc. Silverspring, Maryland, USA, calibration according to ISO standard 12099 ('ISO 12099: Animal feeding stuffs, cereals and milled cereal products — Guidelines for the application of near infrared spectrometry' 2010) as a measure of yield quality. Farmer's potential economic gain [€ ha^{-1}] based on the actual market price for rape-seed oil in 2014 in Switzerland (Swiss granum 2014) was calculated as seed mass [t ha^{-1}] × oil content [g kg^{-1}] × market price [€ ha^{-1}].

Statistical analysis

The response variables 'yield', 'oil content', 'farmer's potential economic gain', 'total number of shoots per plant' and 'flowering onset' were analysed with linear mixed effect models (LMM) using the *R*-package *lme4* (Bates *et al.* 2014) with treatments 'pollination' and

'pest control' and their interaction as fixed and 'block' as random effects. 'Fruit set', 'seed set', 'mean seed mass' and 'total seed mass per fruit' were analysed by means of LMM with the same model structure described above and the additional random factors 'shoot' nested in 'plant'. 'Number of visits per flower lifetime', 'visitation rate' and 'visit duration' were modelled only for cages with pollinators using LMM with 'pest control' treatment as fixed and 'block' as random effect. Residual variances of all models were homoscedastic and normally distributed except those of 'visitation rate', which were log-transformed to meet LMM assumptions. The *P*-values for fixed effects were calculated based on residual degrees of freedom estimated with the Kenward-Roger approximation (Zuur *et al.* 2009).

As parameter estimation in (linear) mixed effect modelling is at the frontier of statistical research, we cross checked the robustness of the model predictions by also estimating all the parameters from these models in a Bayesian framework. Figures show means of posterior distributions from 10'000 samples drawn from three MCMC in JAGS (Plummer 2003) ± the respective standard deviations. Priors were set vague as flat normal distribution with standard deviation of 1,000,000. All statistical analyses were performed in R 3.1.1 (R Core Team 2015).

Results

Synergistic pollination-pest control effects on yield, oil content and farmer's potential economic gain

In the absence of pollinators, OSR yield (total seed mass), oil content and farmer's potential economic gain were increased by 6%, 1%, and 7%, respectively, at strong compared to weak pest control levels (Fig. 1; Table 1). Furthermore, pollination by bumblebees significantly increased OSR yield by 7% on average and farmer's potential economic gain by 7% at weak pest control. Although no effect of pollination on oil content was detected at weak pest control, pollination resulted in a 1.1% increase under strong pest control conditions (Fig. 1; Table 1). Importantly, the positive effect of pollination was significantly stronger at stronger pest control (Fig. 1). This synergistic effect (positive interaction) of pollination and pest control accounted for a pronounced increase in yield (11 %) and farmer's potential economic gain (12%), and a slight but significant increase in oil content (3%) (Fig. 1; Table 1).

The reduction in yield due to lower pest control was caused by an overall reduction in the number of fruits per plant (fruit set), irrespective of the level of pollination (Fig. 2a; Table 1). Yield increase due to pollination, on the other hand, was driven by an increase in the number of seeds per fruit (seed set) (Fig. 2a; Table 1), resulting in a higher total seed mass per fruit, despite a slightly reduced mean seed mass under the pollination treatment (Fig. 2b; Table 1). The positive effects of pollination on seed set and consequently total seed mass per fruit were significantly stronger at strong pest control, indicating that increased seed set per fruit, together with the higher number of fruits, was the principal driver of the synergistic effects of pollination and pest control on OSR yield.

Mechanisms driving synergistic pollination-pest control effects

To detect potential changes in flower visitation behaviour of the pollinators as a response to different levels of pest control (M1), flower visitation rate and visit duration were analysed. However, there was no significant difference in the flower visitation rate or the duration of visits between pest control treatments (Fig. 3; Table 1). To detect potential compensatory growth mechanisms of plants exposed to different levels of pest control treatments (M2), the numbers of side shoots and flowers per plant were analysed. However, there was no indication of over-compensatory growth as the number of fruits decreased with weak pest control and the numbers of shoots did not differ between treatments (Fig. 2a; Table 1). Moreover, flower onset did not differ between pest control treatments (Table 1). However, the estimated number of visits an individual flower received during its lifetime (M3) was reduced by 41% under weak pest control (Fig. 3; Table 1).

Discussion

We found strong synergistic effects between pollination and pest control on the quantity and quality of OSR yield. These positive interactive effects contributed 1.6 and 2.3 times more to quantitative yield gains (total seed mass) than their individual effects respectively. We found significant synergistic effects of pollination and pest control not only on seed set and total seed mass, but also on the oil content of seeds. Although the increase in oil content due to this interaction was rather small (15 g, equivalent to 2.2 %), the gain in harvested oil is highly economically relevant, in particular when considering the vast areas planted with OSR in Europe and worldwide. Insect pollination has also been found to affect oil content and nutritional quality in other oil crops, e.g. almonds (Brittain *et al.* 2014), but the underlying mechanisms of this remain poorly understood. For plants, investing in grain fitness by increasing its fat content is a possible way to strengthen offspring fitness, in particular if pollination occurs through outcrossing (Moles & Westoby 2006). Interestingly such effects on oil content were only detected at low pest levels (Fig. 1b), possibly because a plants' ability to allocate resources is otherwise exhausted by the need to compensate for pest-induced damage. Due to the combined increase of yield quantity and quality, the economic gain for a farmer resulting from the synergistic effect of the two ES (€ 311 ha^{-1}) was 1.7 and 1.8 times that of the individual benefits from pollination (€ 118 ha^{-1}) and pest control (€ 110 ha^{-1}) respectively.

Pest control and pollination driving yield

Pest control and pollination affected OSR yield through distinct pathways: pest control resulted in an increased yield through an increased fruit set (12 % reduced flower abortion at strong pest control), while pollination did not affect fruit set. In contrast, pest control had no effect on the number of seeds per fruit when pollinators were absent (Fig. 2a), whereas pollination increased seed set, with significantly more pronounced increases under strong pest control. This increase in the number of seeds per plant, due to a higher number of seeds per fruit and an increased number of fruits, was the major driver of overall quantitative yield

gains. These findings corroborate recent evidence that insect pollination can significantly enhance seed set and yield in commonly grown OSR varieties (Jauker & Wolters 2008; Bommarco, Marini & Vaissière 2012; Hudewenz *et al.* 2013; Lindström *et al.* 2015). Moreover, and most importantly, they demonstrate that these yield gains strongly depend on the level of pest control. Indeed, pollination increased average seed set from 12 to 16 seeds per fruit under weak pest control, but up to 22 seeds per fruit under strong pest control. Our analysis reveals that although mean seed mass was slightly reduced where more seeds were produced per fruit, a pattern in line with previous studies in OSR (Åhman, Lehrman & Ekbom 2009), this decrease was by far outweighed by the marked increase in seed number, such that the total seed mass per fruit was still significantly higher when pollinated by insects (Fig 2b).

Pest-induced reduction in flower lifetime as a key driver of synergistic pollination-pest control effects

Research on the reproduction of wilds plants proposes a multitude of potential pathways for synergistic processes between pollination and pest control. For example herbivory, and in particular florivory, may modify flower traits such as flower display or floral resource quality (Poveda *et al.* 2005). Alternatively, florivores may directly repel pollinators. Both of these processes can lead to altered plant attractiveness to pollinators (Lehtil, Strauss & We 1997; Strauss 1997) and consequently to reduced flower visitation and pollination (Krupnick, Weis & Campbell 1999). Although bumblebees were confined to cages in our study and were thus only exposed to a reduced set of possible flowers to visit, there were many flowers free of pollen beetles available, which could have preferentially been visited by bumblebees. Selective flower visitation would have forced bumblebees to spend more time searching for pollen beetle-free flowers and hence would have resulted in reduced visitation rates or altered flower visit duration. We could, however, not detect any sign of altered flower visitation behaviour across pest control treatments, indicating that this potential mechanism

(M1) did not play a significant role in explaining the pronounced synergistic effects found in our study.

Another possible pathway driving synergistic pollination-pest control interactions involves compensatory responses of plants to florivory (M2) (Munguía-Rosas *et al.* 2015). If over-compensation had contributed to the observed synergistic pollination-pest control interactions, either the number of shoots or the number of fruits produced per shoot should have increased with pest levels or plant damage levels, resulting in overall higher yields. However, since the number of shoots remained unaffected, and the number of fruits decreased with decreasing pest control, over-compensation should therefore not have played a major role in contributing to the observed interactive effects in our experiment either.

Furthermore, it is conceivable that the amount of pollen available for pollination could be reduced by florivores or pollen thieves to such an extent that pollination success becomes compromised (Hargreaves, Harder & Johnson 2010). Although we cannot exclude the possibility that this pathway contributed to the strong pollination-pest control interactions found in our study, the fact that OSR flowers produce large amounts of pollen (Cresswell 1999) and many flowers remained uninfested by pollen beetles, including in the cages with high pollen beetle densities (Sutter, personal observation), may suggests that the pollen pool available for pollination was probably sufficient and this interaction pathway therefore probably did not play a major role in our study.

Here, we propose an alternative and ─ to our knowledge ─ novel mechanism as the principal driver of the strong synergistic interactions of pest control and pollination: florivory-induced reduction in flower lifetime (M3). Acceleration of flower senescence in OSR occurs via the removal of pollen from the stamens, rather than pollen deposition on stigmas (Bell & Cresswell 1998). Our findings provide a strong indication that pollen beetles trigger such accelerated flower senescence through their removal of pollen from stamens. Pollen beetles reduced flower lifetime by an average of 50% at high compared to low densities. This

shortening in flower lifetime, demonstrated in a complementary experiment specifically designed to test this hypothesis (see Fig. S1 for detailed results), reduces the estimated average number of pollinator visits a flower receives during its lifetime from 2.0 to 1.2 visits. This decrease in total pollinator visitation was associated with a decline in seed set of 26 %. At an average number of pollinator visits of 1.2 at low pest control, a large proportion of flowers are likely to remain unvisited, probably contributing to the observed reduction in seed set. Lower total pollen deposition, lower proportions of outcross pollen and disadvantages due to weaker pollen competition (Burd 1994; Mitchell 1997) may have thereby reduced the seed set. This should be most pronounced when pollinator densities are limited in real agroecosystems; a recent study indeed indicates that enhancing pollinator densities can increase oilseed rape yield, at least in the studied region (Lindström *et al.* 2015).The aim of the present study was to experimentally test a set of possible mechanisms that act on a local scale (M1-M3). However future work should also address other potential pathways of interactions on a larger scale (field or landscape), including direct interactions between pollinating and pest control-providing organisms, which may reveal additional pathways for interactive pollination-pest control effects that have not been studied here. Whilst controlled experiments allow for rigorous hypothesis testing, a potential drawback is the limited applicability of findings to real-word systems. In the present experimental study however, we believe this potential limitation is minimized by (I) using two different, naturally occurring levels of pest control , (II) calibrating pollinator visitation rates based on own and published field data of natural visitation rates and by (III) measuring yield parameters according to standard agronomic practice. Hence, yield and other crop plant parameters, as well as crop damage and pollinator visitation rates are all in the range reported in other field studies (e.g. Bartomeus, Gagic & Bommarco 2015). It is important to measure agronomic metrics of yield because damage or effects on seed set do not necessarily translate into crop yield (Klein *et al.* 2014).

Conclusions and implications

Our study clearly shows that insect pollination and pest control can interact in highly non-additive ways with profound consequences on crop yield and economic value. To improve predictions of the contribution of pest control and pollination to crop yield, current models (e.g. Jonsson *et al.* 2014) should be refined by integrating these interactions. Our results could provide a basis for such improved predictions of OSR yield. It remains an important challenge for future ES research to obtain such data for other important crops in a range of agro-ecosystems. Without taking non-additive interactions among multiple ES into account, estimations of ES and their use in single and multiple ES models (Nelson & Daily 2010), spatial ES value mapping (Ricketts & Lonsdorf 2013) or benefit transfer functions (Plummer 2009) are not reliable and can even be misleading. Our findings also have profound implications for ecosystem management (Cimon-Morin, Darveau & Poulin 2013). Although the drivers of pest control and pollination in agro-ecosystems have been studied well in isolation, there is evidence that shared drivers, such as land-use change, can jointly affect multiple ES (Schröter *et al.* 2005). Our findings highlight that the effectiveness of measures aimed at mitigating pollinator losses, to enhance crop pollination services, may fail to deliver economic yield benefits if pest control services are not concomitantly addressed. In contrast, integrated management of multiple ES could be a promising and cost-effective approach towards ecological intensification (*sensu* Bommarco, Kleijn & Potts 2013) by taking full advantage of synergies among multiple ES. Yet, to effectively and sustainably manage agro-ecosystems for multiple ES, more research aimed at a better understanding of the interactions among ES is vital.

Data accessibility

All data associated with this manuscript is available at the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.gm11d

Competing interests

We have no competing interests.

Author contributions

LS and MA designed the study, LS and MA performed the research, LS analysed the data, and LS and MA wrote the manuscript.

Acknowledgements

We thank Stephan Bosshart and Amélie Mandel for their help with the fieldwork and Carolin Luginbühl and Philipp Walther for technical advice regarding OSR cultivation. We are grateful to James Cresswell, Felix Herzog, Phillippe Jeanneret, Steven Johnson, Owen Petchey, Dirk Sanders, Bernhard Schmid and Matthias Tschumi and two anonymous reviewers for valuable discussions and helpful comments on an earlier version of the manuscript and Sarah Radford and Katherine Horgan for improving the language and writing of this article.

Funding

This project has received funding from the European Union's Seventh Framework Programme for research, technological development and demonstration under grant agreement N° 311879.

Figures and Tables

Figure 1

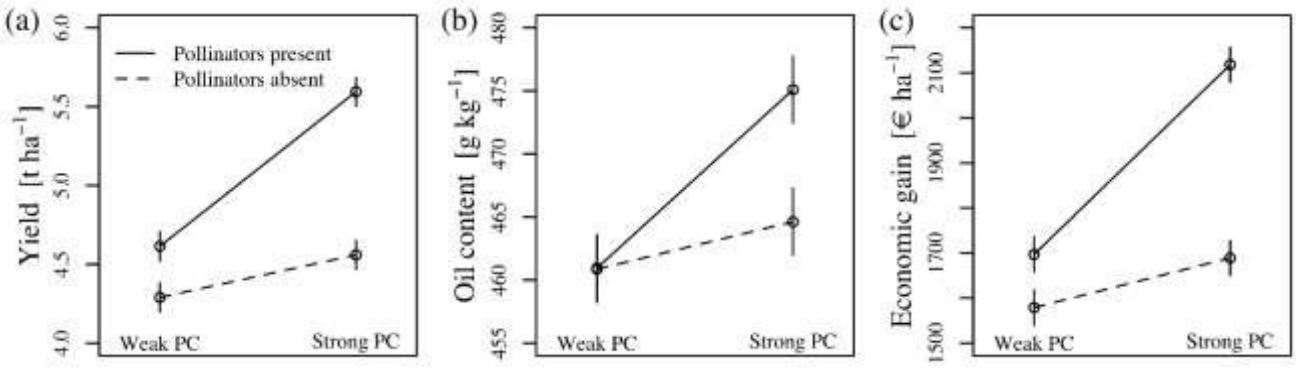


Figure 1 Mean of posterior distribution ± SD of (a) oilseed rape yield, (b) oil content and (c) farmer's potential economic gain with 'insect pollination' (bumblebee pollinators present (solid line) or absent (dashed line)) under weak vs. strong pest control (PC) (n = 6).

Figure 2

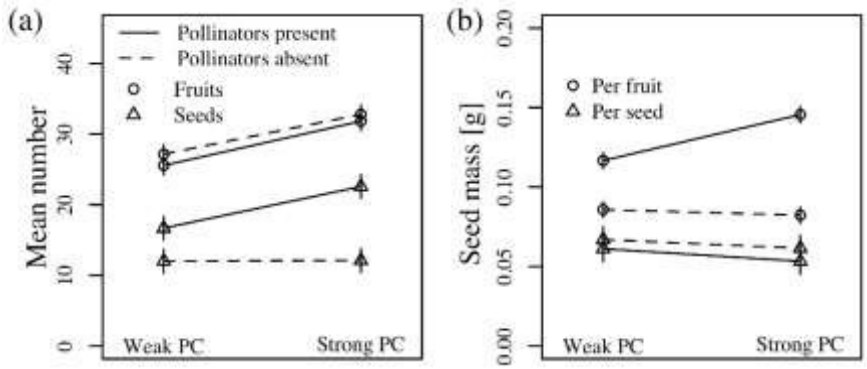


Figure 2 Mean of posterior distribution ± SD of (a) seed set per fruit (triangles) and number of fruits per shoot (fruit set; circles) and (b) mean seed mass per seed (mean mass of 10 seeds for display, triangles) and total seed mass per fruit (seed set × mean seed mass per seed, circles) of oilseed rape as a function of insect pollination (bumblebee pollinators present (solid line) or absent (dashed line)) under weak vs. strong pest control (PC) (n = 6).

Figure 3

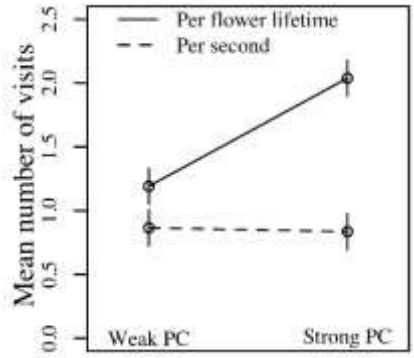


Figure 3 Mean ± SD of posterior distribution of the average number of oilseed rape flowers visited by bumblebee pollinators per second (average visitation rate; dashed line) and the predicted number of pollinator visits per flower lifetime (solid line) under weak vs. strong pest control (PC) (n = 6).

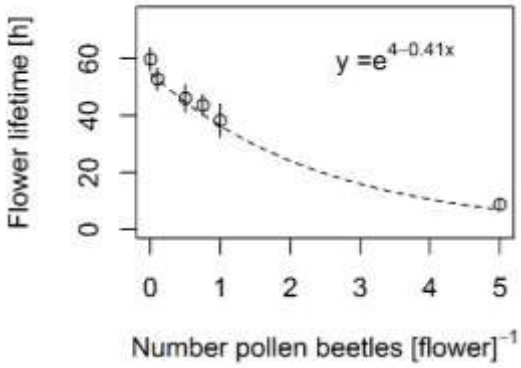
Table 1 Summary of the results of linear mixed effect models testing the effects of the fixed factors 'insect pollination' (bumblebee pollinators present or absent), 'pest control' (weak vs. strong pest control (PC)) and their interactive effect on investigated response variables. The response variables 'flowering onset', 'visits per flower lifetime', 'visitation rate' and 'visit duration' were only assessed for the 'pest control' treatment. Denominator degrees of freedom (*DDf*), *F*-values and corresponding *P*-values from linear mixed effect models, based on Kenward-Roger approximations, are shown (see Materials & Methods section for detailed description of explanatory variables, response variables and statistical models).

	DDf	*F*-value	*P*-value
Yield (total seed mass ha^{-1})			
Pollination	10.60	66.69	**<0.001**
Pest control	12.58	52.54	**<0.001**
Pollination × pest control	17.01	13.94	**0.002**
Oil content			
Pollination	12.08	4.33	0.059
Pest control	14.99	11.67	**0.004**
Pollination × pest control	14.99	3.96	0.065
Farmer's potential economic gain			
Pollination	11.74	56.31	**<0.001**
Pest control	14.40	49.84	**<0.001**
Pollination × pest control	15.55	16.24	**<0.001**
Number of fruits			
Pollination	12.08	0.97	0.344
Pest control	14.99	20.22	**<0.001**
Pollination × pest control	14.99	0.06	0.816
Seed set			
Pollination	11.94	124.72	**<0.001**
Pest control	14.75	18.58	**<0.001**
Pollination × pest control	15.23	16.83	**<0.001**
Mean seed mass			
Pollination	11.28	8.34	**0.014**
Pest control	13.65	6.50	**0.023**
Pollination × pest control	16.18	1.77	0.201
Total seed mass per fruit			
Pollination	12.08	93.42	**<0.001**
Pest control	14.99	6.42	**0.023**
Pollination × pest control	14.99	10.46	**0.006**
Total number of shoots per plant			
Pollination	219.69	1.46	0.229
Pest control	184.76	0.81	0.370
Pollination × Pest control	23.01	0.22	0.645
Flowering onset			
Pest control	16.01	0.98	0.337
Mean number of visits per lifetime			
Pest control	10.00	7.84	**0.008**
Visitation rate			
Pest control	10.00	0.07	0.792
Visit duration			
Pest control	10.00	0.14	0.712

Supporting Information

Appendix S1 Results of an experiment with potted OSR plants to quantify the relationship between flower lifetime of OSR and the number of pollen beetles per flower. The exponential reduction of flower lifetime with increasing pollen beetle density per flower is adequately described by a linear relationship ($y = e^{4-0.41x}$) between log-transformed flower lifetime and pollen beetle density ($DDf = 58$, $F = 167$, $P < 0.001$, $R^2 = 0.74$). Circles show means ± SEM of 10 replicates per pollen beetle density treatment.

Figure S1



DISCUSSION

Louis Sutter


Photo N. Boo

General discussion

To set the presented results in mutual context together with emerging ideas, this chapter will follow the functional chain of ecosystem services in agro-ecosystems highlighting important stages, and suggests new questions and targets, aiming towards evidence-based research for sustainable agriculture. It will explore: (i) The availability of resources in agro-ecosystems, (ii) local ecosystem service delivery as a function of landscape composition and (iii) synergies and trade-offs amongst ecosystem services.

Availability of resources in agro-ecosystems

Lack of a food resource can be one factor forcing wild populations to decline (Kleijn & Raemakers 2008). Through the introduction of elements managed to enrich plant assemblages, implemented to slow down or reverse the loss of biodiversity that arises from intensification by modern agriculture (e.g. agri-environmental schemes or greening measures), it is possible to provide resources to a broad variety of organisms simultaneously (chapter 1; Senapathi *et al.* 2015b). The results from chapter 1 suggest in addition that increased plant species richness, a possible outcome of ecological enhancement of herbaceous vegetation in agro-ecosystems (Knop *et al.* 2005; Aviron *et al.* 2009), provides food resources to different target groups, although their resource preferences are not congruent. Despite similar resource use, marked preferences were found, especially when comparing wild and managed service providers. A fact which stresses the distinction made between honey bees and wild bees regarding conservation actions (Scheper *et al.* 2013; Senapathi *et al.* 2015a). This distinction is also supported by the fact that honey bees and wild crop pollinators did not react similarly to changes in landscape complexity (chapter 2). Wild pollinator abundance increased with an increasing proportion of semi-natural habitats, whereas honey bees showed no such relationship, probably because honey bees are less dependent on resources provided by such ecological infrastructures (Steffan-Dewenter *et al.* 2001), since they are actively managed by

bee keepers. The result that the abundance of key resources is stronger in determining bee abundance than total resource abundance is decisive for pollinator restoration management, because not the total amount of food, but the presence of particular species within the flowering community is important. The identification of preferred key plants for different bee groups lead to an expedient way of directly measuring the success of conservation actions for a target group, and allows the inclusion of such species in seed mixtures for targeted flowering enhancements. Chapter 1 shows resource delivery of herbaceous semi-natural habitats to bees, the main group of pollinators in this system, yet the question remains whether it is possible to transfer such a pattern to other service providers like pest antagonists (Wratten *et al.* 2012). Grass *et al.* (2016) showed that the floral resources provided by flower strips targeted for pollinator mitigation were steadily used by several groups of pest antagonists in varying landscapes. Although it was not possible to clearly identify the parameter that increased the abundance of predators in chapter 2, it is plausible that pest antagonists may profit from the same resources as pollinators at landscape or regional level but rely on additional resources (Shackelford *et al.* 2013).

Habitats created to mitigate biodiversity loss, like agri-environmental schemes provide resources on several levels: shelter, optimal micro-climate conditions or undisturbed overwintering sites (Bianchi, Booij & Tscharntke 2006; Sarthou *et al.* 2014). The provided resource spectrum necessary to support ecosystem service providers could be regarded from an insurance perspective, similar to the concept of species redundancy in biodiversity ecosystem-function-research (Naeem & Li 1997). If many functionally different resources overlap in space and time, a transitional unavailability of one resource type should allow individuals relying on this resource to find an acceptable replacement nearby, without severe fitness consequences. Timing of resource availability is an important aspect to consider (Schellhorn, Gagic & Bommarco 2015). The results in chapter 1, where the total amount of

resources did not define the success of a mitigation measure, but rather the presence and abundance of key species under the umbrella of a functional complementarity of plants, could be applied to the temporal dimension. It is possible that the continuity of resources rather than their total amount determines the population size and its ability to provide an important service (e.g. control of a pest before infestation). If a shortening in a resource provision arises during the exponential growth phase (Vandermeer 2010), the provoked delay in reaching the carrying capacity – the moment where pest antagonists are able to control the prey – is substantially longer and pest control acts too late, when crop damage has already occurred. Bottlenecks and interruptions in the provision of key resources that affect the population growth of service providers should therefore be identified (Schellhorn, Gagic & Bommarco 2015). Once known, these resource gaps can be filled, which should eventually increase stock, flow, and stability of ecosystem services, making the general prescription of increasing natural or semi-natural habitats more efficient.

Local ecosystem service delivery as a function of landscape composition

Agricultural fields can be compared to barren islands (Denys & Tscharntke 2002), because local communities are dependent on regional diversity and are mostly unsaturated (Holt, Gaston & He 2002). Therefore, the local assemblage of service providers depends on the recruitment of species to fill the locally available niches (Folke, Holling & Perrings 1996). The proportion of species from the regional pool which can be expected in agricultural fields is rather low, because of their high level of disturbance (Bengtsson *et al.* 2003). The long-term stability of local ecosystem service delivery is at risk, particularly in structurally simple landscapes, if the set of species necessary to provide a reasonable function are absent (Hunter 2002). Thus, it is not expected that bees – *a priori* more mobile – are more affected by local flower planting than ground beetles (chapter 2, Fig. 1). One explanation for this

pattern could be that pollinators are fundamentally more attracted to forage in mass flowering crop fields because the resource provision – nectar and pollen *ad libitum* – is obvious (Westphal, Steffan-Dewenter & Tscharntke 2003). Predators on the other hand, generalists in particular, should not expect larger amounts of food in such a field compared with any other crop field. One aim of mitigation measures is to attract service providers from habitats where they overwinter, into the fields when they are needed. Local ecological infrastructures serve as stepping stones for service providers, advertising that suitable conditions can be found (Duelli & Obrist 2003). However, the success of this concept builds on the fact that the regional stock of service providers is large, stable, and diverse. If regional semi-natural habitats are degraded or non-existent, it might be inefficient to implement local measures (Kennedy *et al.* 2013). If service providers were not present anymore because their habitats have been degraded too much or cultures are grown in areas where service providers naturally not occur, an uneconomical workaround – not a solution – would be an inundation of service providers through human management (Bale, van Lenteren & Bigler 2008).

Synergies and trade-offs among ecosystem services

Ecosystem services are clearly not independent. Chapter 3 shows clear synergistic effects between insect pollination and simulated pest control. These positive interactive effects contributed more to final ecosystem service – higher crop yield – than the regulating services themselves. Although in chapter 2, no clear interactive effects could be detected the due to the high complexity in this natural study system, the fact that both services did not react identically to landscape changes (chapter 2, Fig. 1) indicates that it is of common interest to monitor many services simultaneously. Therefore, questions about insect pollination and natural pest control – ideally along with other potentially interfering functions – should be addressed at the same time, whether the goal is to restore biodiversity or optimise crop production (Seppelt *et al.* 2011). Considerable value should be attached to efforts made to

create bundles of ecosystem services for analysis of trade-offs (Raudsepp-Hearne, Peterson & Bennett 2010) or indices of multifunctionality where many services are aggregated (Wagg *et al.* 2014; Allan *et al.* 2015). In this study the focus lies on regulating services, primarily because provisioning services are better studied (Howe *et al.* 2014) and additionally because changing ecosystem components, which generate regulating services, may undermine the long-term existence of provisioning services (Carpenter *et al.* 2006). Future work should additionally encompass potential synergies on other scales and other ecosystem service groups and include synergies into estimations and ecosystem modelling (Nelson & Daily 2010). There is no prediction that interactions among ecosystem services should be positive, trade-offs occur as well (Fisher *et al.* 2011). For instance, the provision of an ecosystem service can be narrowed due to the increased provision of another (Rodríguez *et al.* 2006). As demonstrated in chapter 3, the identification of mechanisms behind trade-offs is crucial and research on ecosystem services proposes a multitude of pathways for interactive effects. An understanding of the mechanisms underpinning ecosystem service delivery and therefore trade-offs and synergies requires a framework, such as that developed by Bennett *et al.* (2009). Once many mechanisms are identified the goal is to identify common patterns or similarities in mechanisms predicting trade-offs or synergies for co-occurring ecosystem services directly (Howe *et al.* 2014). These might be shared drivers, such as land-use change, because they jointly affect several ecosystem services (Schröter *et al.* 2005), or they might be inherent to stakeholders benefiting from the ecosystem service. Future studies should particularly consider trade-offs and synergies at a large scale between ecosystem service provision, food production and biodiversity conservation needs.

Finally, predictability of ecosystem services should be improved by including dynamics in ecosystem service modelling and prediction. Shared drivers like environmental change, feedbacks or unexpected dynamics in food webs can lead to unforeseen outcomes (Rodríguez *et al.* 2006; Dobson *et al.* 2006; Nicholson *et al.* 2009). Such feedbacks may

intensify – or be intensified by – anthropogenic modifications of ecosystems leading to ecosystem degradation (Carpenter, Bennett & Peterson 2006). There is a considerable lag in ecosystem service feedback compared to valuation signals in the economy, which respond much faster (Tallis *et al.* 2008). Ignoring ecological underlying forces may increase risks of regime shifts altering the capacity of an ecosystem to provide services for future generations (Carpenter, Bennett & Peterson 2006; Bennett *et al.* 2009; Nicholson *et al.* 2009).

Conclusions

Ecosystem services are crucial for past, current and future human well-being and have varying strength depending on time, geographical situation, and other ecosystem services. They can be positively influenced with adequate management or planning of the agricultural matrix. Service providers are animals with complex live cycles and multi-layered requirements which have to be accounted for. If these requirements are not understood and provided through natural processes or active management, populations may collapse with no guaranty of recovery. However, ecosystem service delivery should not be the only argument for the implementation of mitigation measures because biodiversity conservation is equally important and can – at least under some circumstances – be fostered in parallel. To have effects on crop yield, which is an implicit aim of research on ecosystem services, ecosystem services delivery has to be very strong in order to overlay effects of local management, climate variability or other varying factors that are predominant. Finally, research agendas must recognise that ecosystem services are not independent and more research on trade-offs has to be carried out. Situations where trade-offs are more probable than synergies, might occur in the future, have to be identified quickly to anticipate decision making and defuse trade-offs in an anticipatory way.

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ACKNOWLEDGMENTS

First of all, I would like to thank you, Matthias and Philippe for the being great supervisors over the past years. I am grateful for all of the sound science I have learned from you, but equally for your presence and readiness to discuss, read and comment on my work and motivate me whenever I needed it. Both of you are excellent scientist and exceptional companions. Not to mention that without your advice and patience this thesis would not be in your hands today. I am convinced that you have managed particularly well to find the balance between promoting my independence to develop own ideas and providing guidance where needed. Further, I wish to thank my additional supervisors and committee members and Owen and Bernhard for the discussions, constructive meetings and sharing your immense experience in ecological research and environmental sciences. I thank all the people in our research group, with particular thanks to Felix, for fine tuning manuscripts. Without the overwhelming technical support from Stephan, Caroline, Phillip, Fritz and the entire Feldgruppe to realise my, I agree, sometimes unconventional ideas, I would not have been able to conduct all these experiments, you were a tremendous help for me. Thanks to my fellow PhD students at Reckenholz: Nina, Gisela, Bärbel, Sonja, and Lolitta who were always around for a chat or to help in the field on peak days. I thank the master students Amélie, Maëva, and Mike who accompanied me for months in my project for your curiosity, endurance, and fruit bearing thoughts. I wish to thank all QuESSA project partners for the enriching experience of a close international collaboration with hot debates, cold beers, and stimulating meetings. Many results I have presented would not be here without the help of these GIS-experts: Alessandro, Raphael, Dario, Erich, Jonas, Sebastian, thank you! I owe thanks to Andreas Müller, Ruth Bärfuss, Sonja Gerber, Werner Marggi und Karin Schneider for entomological advice. The following list of people I want to thank for standing hours in the field or lab along with me and supporting the project with their sweat over these years: Matthias Bleisch, James Canales,

Mirco Coric, Marc Fässler, Miriam Fischer, Mischa Haas, Adrian Häni, Marco Labarile, Julian Lindenmann, Pasha Naeem, Jonathan Noack, Emanuele Rupf, Tim Seitz, Marco Urech, Remy Vuillemin. The motivation to start such a project was strongly influenced by the friends and former supervisors Eva and Dirk, thank you very much for your mentoring. I wish to thank Sarah and Katie for improving and checking my English. Numerous farmers granted access to their properties for our experiments and without their willingness to participate in this project my thesis would not have been possible. I am especially grateful to Matthias Tschumi for being a friend and mentor and the same time. Your experience, communication and organisational skills were an immeasurable help during the past years. I am deeply grateful to my entourage: To my grandparents Alice und Edi, I wrote substantial parts of this work in your house, to Mueti, Vati, Linda and Urs along with many many friends who supported my undertaking, who helped me to stay focused but also distracted me when necessary and who awoke my curiosity for nature. Finally, and above all I wish to express my most sincere gratitude to you Pauline, for your endless patience, support, and your love.

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Publications

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Review experience

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Field course assistant „Biodiversity Monitoring of Alpine Ecosystem“, led by Prof. Dr. Helmut Brandl, Universität Zürich, Sommer 2013/14/15.

Fundraising:

9800 CHF from Graduate Research Campus of the University of Zürich for organising an international workshop about Ecosystem Services. Together with Katie Horgan and Daniela Braun.